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Observations on the benthic marine algal flora of South Georgia: a floristic and ecological analysis

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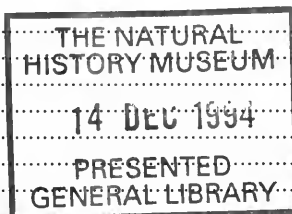
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CONTENTS

Introduction	101
Materials and methods	102
Results	103
Distribution of shore algae	103
Systematic list	103
Discussion	111
Shore ecology	111
Marine algal flora	112
References	113



SYNOPSIS. The pattern of littoral zonation of benthic algae on rocky and boulder shores in Husvik Harbour, on the north-east coast of South Georgia, was investigated during the austral summer of 1990/91. Distribution patterns are similar to those on other shores in the sub-Antarctic region of the Southern Ocean, except for the absence in the littoral fringe of a 'Hildenbrandia' or 'Hildenbrandia-Bostrychia' association'. The supralittoral fringe is devoid of macroalgae and gives way to a eulittoral zone consisting of a series of belts. An uppermost belt dominated by *Porphyra* followed by ones dominated or co-dominated by *Nothogenia fastigiata*, *Iridaea cordata*, and *Adenocystis utricularia*. The lowermost belt is either dominated by *Palmaria georgica* or co-dominated by this red alga and *Schizosieris condensata*. The upper vertical limit of crustose coralline algae and the kelps *Macrocystis pyrifera* and *Durvillaea antarctica* define the sublittoral fringe; the latter is only present on wave-exposed shores. The 103 species of algae known from South Georgia are critically evaluated, four are endemics and 12 are known only from South Georgia and Tierra del Fuego. The biogeographical affinities of the algal flora of South Georgia lies with other sub-Antarctic islands and the southern tip of mainland America.

INTRODUCTION

South Georgia is an isolated island in the Southern Ocean that lies between latitudes 53°56'–54°55'S and longitudes 34°45'–38°15'W. It is roughly crescent-shaped (Fig. 1) and the second largest of the circum-Antarctic islands. Its steep rocky coast, dissected by deep fjords and bays, provides suitable though very hostile habitats for benthic organisms. The algal flora of South Georgia remains little-known since biological exploration has been limited to a few bays on the more sheltered north-east coast. The first publications specifically on its marine algae are those of Reinsch (1888, 1890) and were based on material collected by the 1882–1883 German

International Polar Year Expedition. The next major period of collecting on the island was during the 1901–1903 Swedish South Polar Expedition, but most of the material was lost when the expedition's ship 'Antarctica' foundered. Fortunately, the journals belonging to the expedition's botanist, Carl Skottsberg, survived and he re-visited the island in 1909 to make further observations and new collections. Information contained in his journals was used to write an ecological account of South Georgian algae which was subsequently published (Skottsberg, 1941). Some of the numerous expeditions en route to higher Antarctic latitudes have found safe anchorage at South Georgia and used the opportunity to collect algae from its shores.

Accounts of the ecology of Antarctic and sub-Antarctic

marine algae still remain almost wholly descriptive. Early information on sublittoral assemblages was obtained indirectly by trawling, dredging and the collection of drift plants. The advent of SCUBA diving has enabled direct observations and the hand collection of undamaged specimens of sublittoral algae at several localities in the Southern Ocean (Neuschul, 1968; Délepine et al., 1966; Lamb & Zimmermann, 1977). Unfortunately SCUBA diving to investigate algal ecology has yet to be carried out on South Georgia. Observations on its sublittoral algal ecology date back to the early years of this century and are restricted to dredged collections (see Skottsberg, 1941). Although incomplete and unevenly distributed, there is sufficient information to enable some preliminary conclusions to be reached on the distribution patterns of littoral algae in the Southern Ocean (see Stephenson & Stephenson, 1972; Luning, 1990; Délepine et al., 1966; Zaneveld, 1964). Few experimental studies and the absence of reliable quantitative data have meant that information is lacking on ecological interactions involving algae.

The present study examines the distribution and abundance of shore algae on the north-east coast of South Georgia, critically reviewing all published and unpublished records, and makes some observations on the biogeographical affinities of its algal flora.

MATERIALS AND METHODS

Five transects were studied at Husvik Harbour ($36^{\circ}40'W$,

$54^{\circ}11'S$), Stromness Bay on the north-east coast of South Georgia (Fig. 1). This relatively wave-sheltered bay has small rocky outcrops of volcanoclastic sandstone-shale turbidite (Macdonald et al., 1987) separated by coarse sand or gravel beaches; all its shores are free from ice-scouring. Three of the transects were on rocky shores: A was north of the whaling station and below the catcher boat 'Karrakatta' on its repair slipway; B and C were on the southern side of the Harbour and on the west (B) and east side (C) of Kanin Point (Fig. 1). The other two transects were on boulder shores at Brain Island Point (D) on the northern side of Husvik Harbour and between the Husvik 'villa' and Kanin Point (E) on the southern shore.

The benthic algal communities on shores in Husvik Harbour were monitored at intervals from October 1990 to mid-January 1991. It was considered that by the end of the period the cover abundance of shore algae was close to its seasonal maximum. The distribution and cover of macroalgae were determined between 25 January and 15 February 1991 along the five shore transects. Each transect was surveyed from low water to the top of the supralittoral fringe using an Abney level mounted on a wooden block to give a base to horizontal line-of-sight distances of 20 cm. Slope distance between stations along a transect was measured with a tape. From these data both horizontal and vertical distances between sampling stations were calculated and shore profiles drawn (see Fig. 2). Vertical heights were corrected to Chart Datum (C.D.) using Admiralty Tide Tables (Admiralty, 1990, 1991). The tidal range is c. 1.2 m and the cumulative measurement error was $+0.1$ m at high water mark.

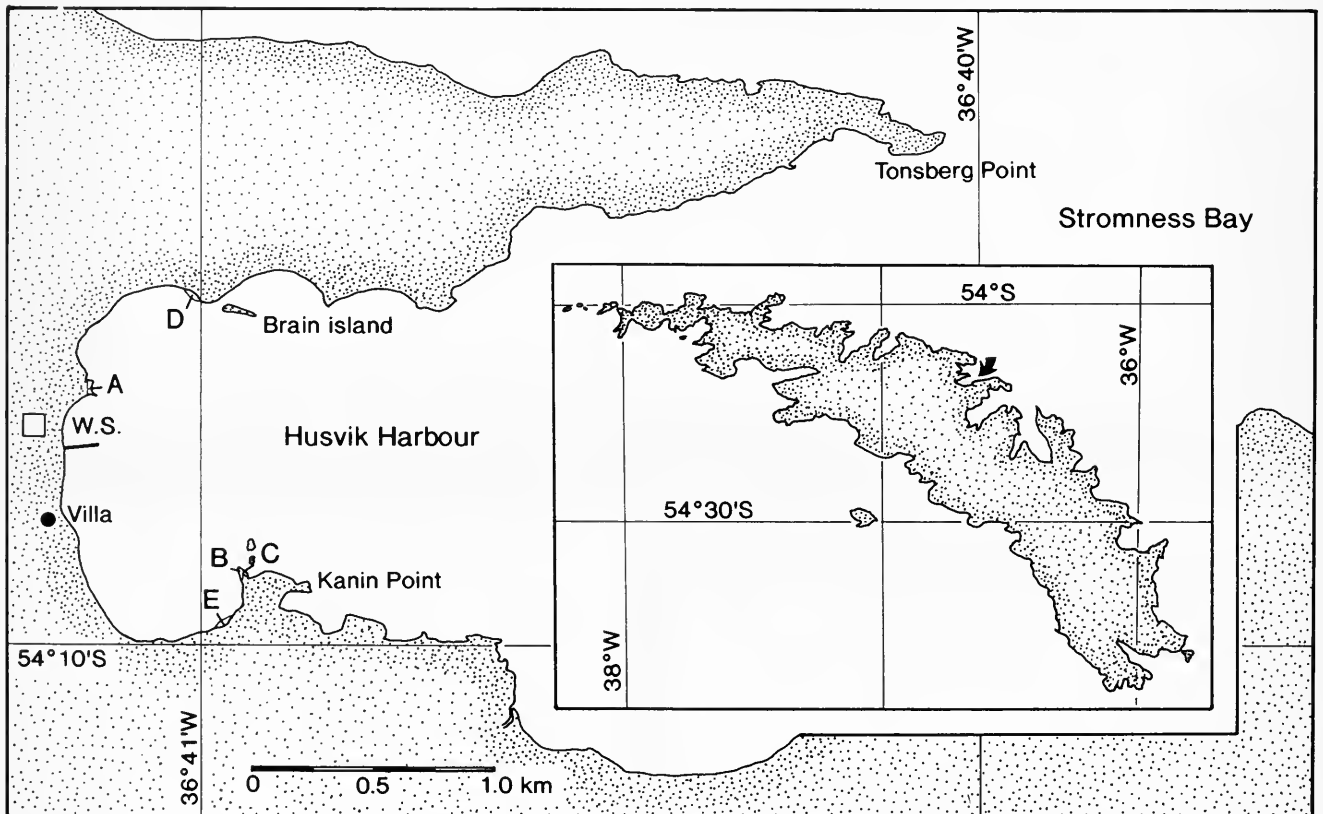


Fig. 1 Map of Husvik Harbour on the north-east coast of South Georgia showing the position of the five investigated transects (A-E). Insert of South Georgia shows an arrow indicating the position of Husvik Harbour. W.S., whaling station.

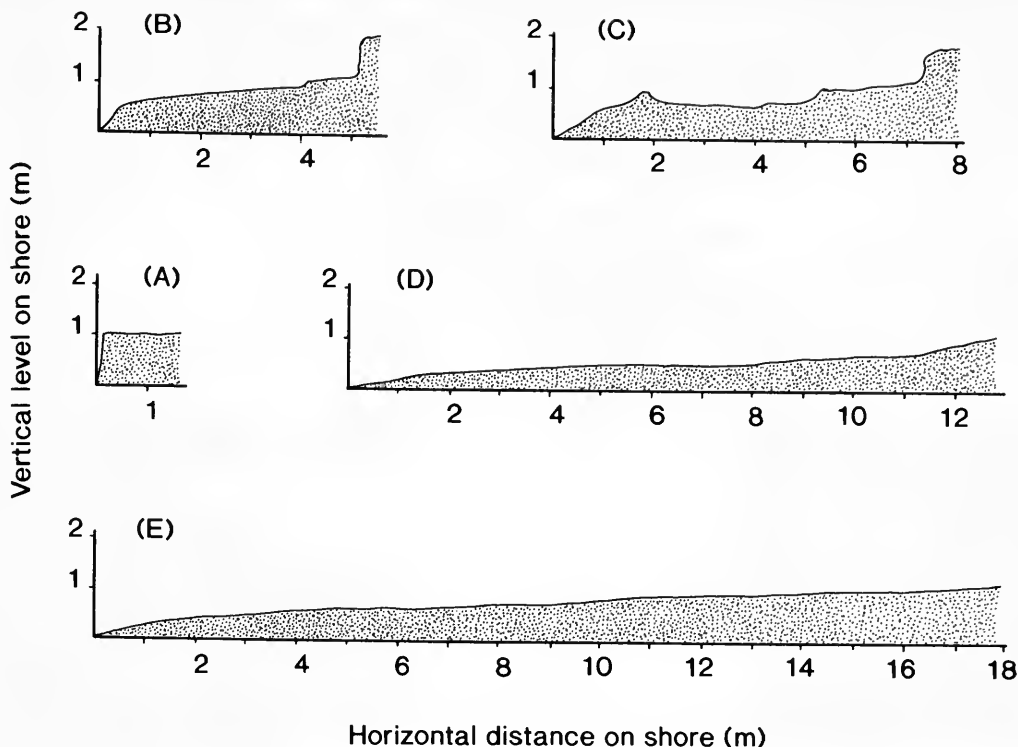


Fig. 2 Shore profiles of the five transects.

The algal assemblages were photographed in situ and all material collected was preserved in 5% seawater-formalin. The relative cover abundance of the dominant macroalgae at each sample station was calculated to within $\pm 3\%$ and expressed as a percentage of total rock covered. All algal specimens are deposited in the Herbarium at The Natural History Museum, London.

RESULTS

Distribution of shore algae

Despite the small tidal amplitude (*c.* 1.2 m) marine influences extend vertically by several metres where the coast is exposed to heavy swells and severe wave action. Only in rocky bays and inlets is the sea sufficiently calm to enable a detailed analysis of the distribution of shore organisms. In Husvik Harbour, the upper limit of the littoral zone is about 1.5–1.7 m above C.D. on rocky shores (Figs 3–5) and 0.75–1.2 m on the boulder shores (Figs 6–7), based on the vertical limit of the membranaceous red alga *Porphyra*. Total algal cover shows considerable variation (Fig. 8) in response to several factors well-known to influence algal abundance and distribution, i.e. shore topography (see Fig. 2), shore aspect, nature of the substratum, and type and degree of exposure to water motion. Rocky shore transect A is partially shaded, faces due south and is positioned along a surge channel. Transects B and C run across rocky shores that are in close proximity to each other (see Fig. 1), the former more wave-sheltered due to the presence of a rock spur. The other two transects (D, E) run over gently sloping boulder shores and most algae are restricted to the sides of the boulders. *Porphyra* accounts for

the high total algal cover on the upper part of the eu littoral zone in transects B and E.

The algal vegetation of the rocky shores (Figs 3–5) comprises 12 to 13 species. The upper eu littoral was dominated by *Porphyra* whose cover-abundance was particularly high on gently sloping shores (B, C; see Fig. 2). Associated with *Porphyra* were *Nothogenia fastigiata* and *Iridaea cordata*; these latter two red algae were found commonly in protected niches. They were not present higher than 1.1 m above C.D. and tended to be confined to the lower part of the *Porphyra* belt. The lower eu littoral zone was dominated by the red alga *Palmaria georgica*, accompanied by lesser amounts of *Porphyra* sp., *Schizoseris condensata* and *Adenocystis utricularis*; the latter grew as isolated clumps or single plants confined to sheltered niches. In the lower eu littoral zone the filamentous red alga *Ceramium rubrum* was frequently intermingled with clumps of *Schizoseris*. Small *Macrocystis* and encrusting calcareous red algae ('lithothamnia') were observed around Chart Datum and below.

Only 7–9 algal species were found on the boulder shores D and E (Figs 6, 7), with the former unusual in having a sparse cover of *Porphyra* and a lower eu littoral zone dominated by colonial diatoms. The brownish layer of diatoms covered the sides of many boulders, occupying the position of the *Palmaria/Schizoseris* association on rocky shores. The upper eu littoral of shore E was dominated by *Porphyra*, confined to the sides of boulders, and the lower eu littoral zone had a very sparse covering of a mixture of algae.

Systematic list

A list of the marine benthic algae from South Georgia based on a critical evaluation of published records, and an examination of material collected by one of us (PJAP) in January and

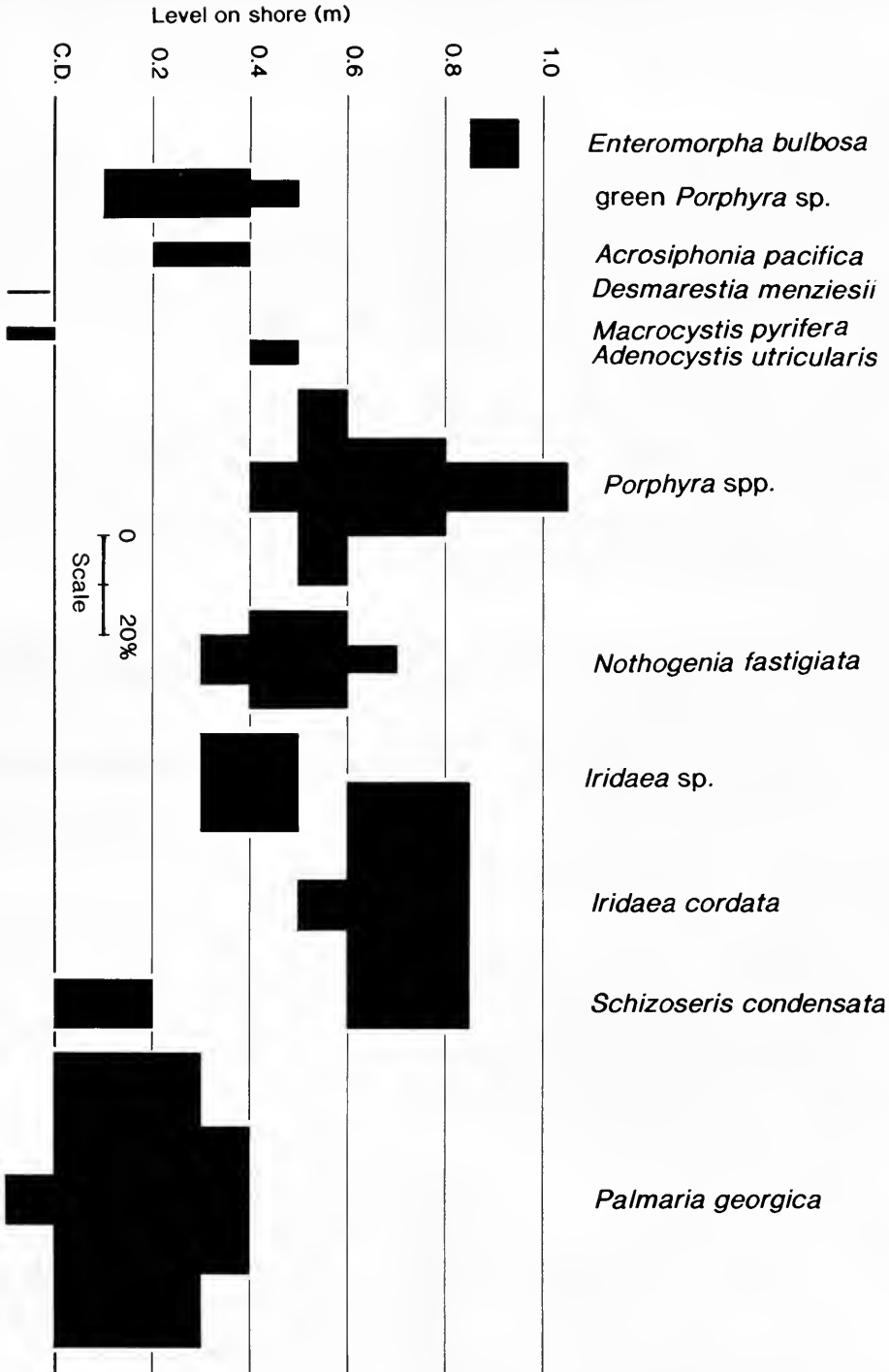


Fig. 3 The vertical distribution and percentage cover abundance of seaweeds on the rocky shore transect A.

February 1991 and specimens in the Herbarium of The Natural History Museum, London. Nomenclatural revisions and re-examination of material has resulted in some of the species listed here published under different names. Given under each entry is the name(s) by which the species has been reported in the list area (synonyms, misdeterminations). For further information on many of the entries, see Papenfuss (1964). Qualifying notes accompany some of the entries

especially where there is an element of doubt attached to the records.

Chlorophyta

Acrosiphonia pacifica (Montagne) J. Agardh
Reported as *Cladophora arcta*, *C. pacifica*, *Spongomorpha arcta* and *S. pacifica*.
Cladophora incompta (Hooker f. & Harvey) Hooker f. & Harvey

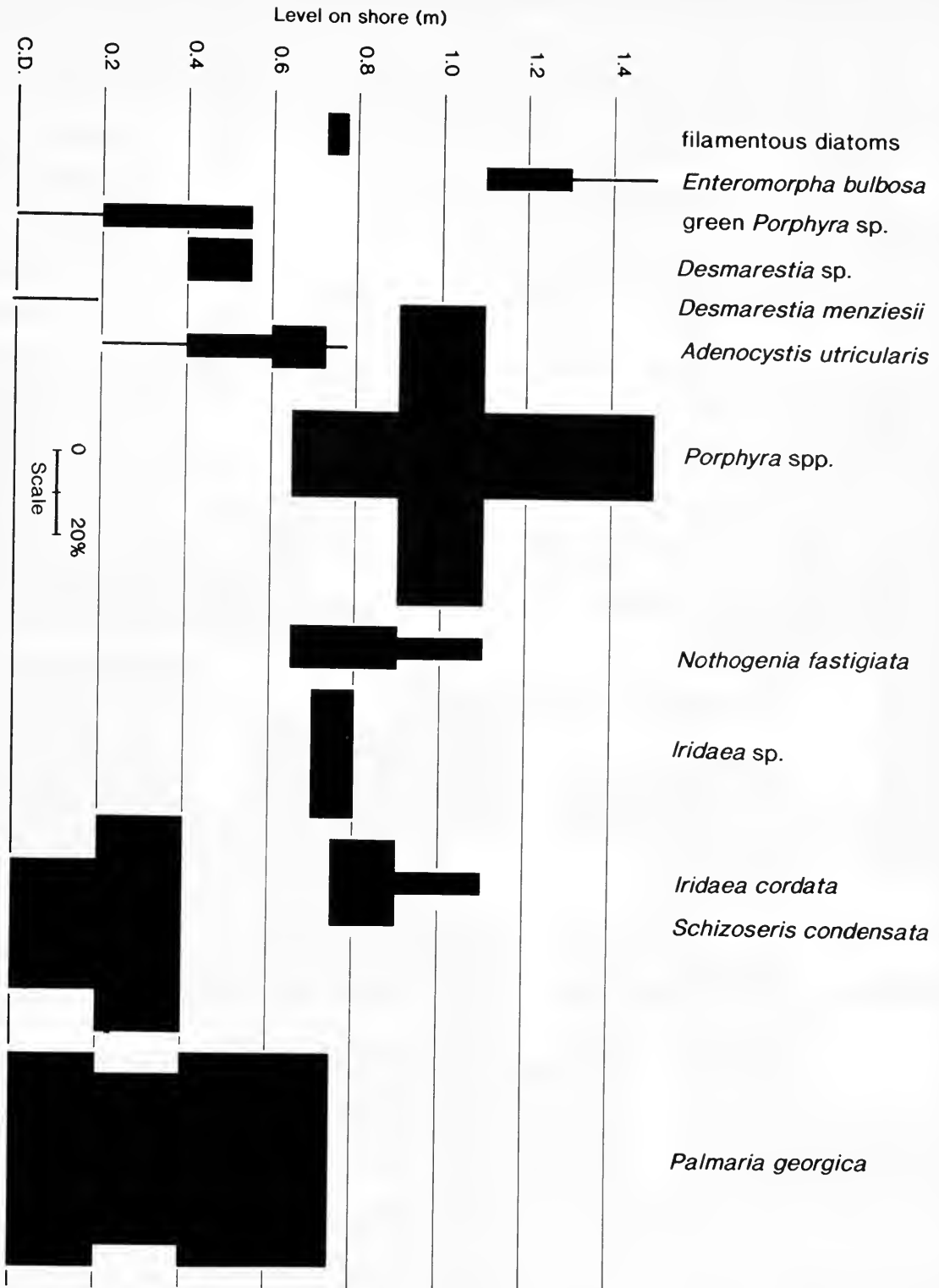


Fig. 4 The vertical distribution and percentage cover abundance of seaweeds on the rocky shore transect B.

Enteromorpha bulbosa (Suhr) Montagne

Reported as *E. novae-hollandiae*.

All plants collected during the Swedish 1907–1909 expedition and attributed to this species by Hylmo (1919) may equally well be a form of *E. intestinalis* (see Ricker, 1987: 36). The principal features distinguishing *E. bulbosa* from *E. intestinalis* are the smaller dimen-

sions of its cells and their thicker walls (Lamb & Zimmermann, 1977), or the absence of any branching of the thallus (Ricker, 1987).

Enteromorpha gunniana J. Agardh

Closely related to *E. bulbosa*, with a plant from Macquarie Island attributed to *E. gunniana* by Ricker (1987: 36) considered to fall



Fig. 5 The vertical distribution and percentage cover abundance of seaweeds on the rocky shore transect C.

within the form range of *E. bulbosa*. Doubt attaches to the species identification of this alga from South Georgia.

Entonema subcorticale Reinsch

This taxon and the following are little-known epiphytes, possibly identical to *Entocladia* (see Ricker, 1987: 24).

Entonema tenuissimum Reinsch

?*Prasiola crispa* (Lightfoot) Meneghini subsp. *antarctica* (Kuetzing) Knebel

Recorded as *P. antarctica*.

Doubtful record as no text entry and yet listed in Reinsch's index (Reinsch, 1890); this is the likely source of Hylmo's (1919) secondary citation.

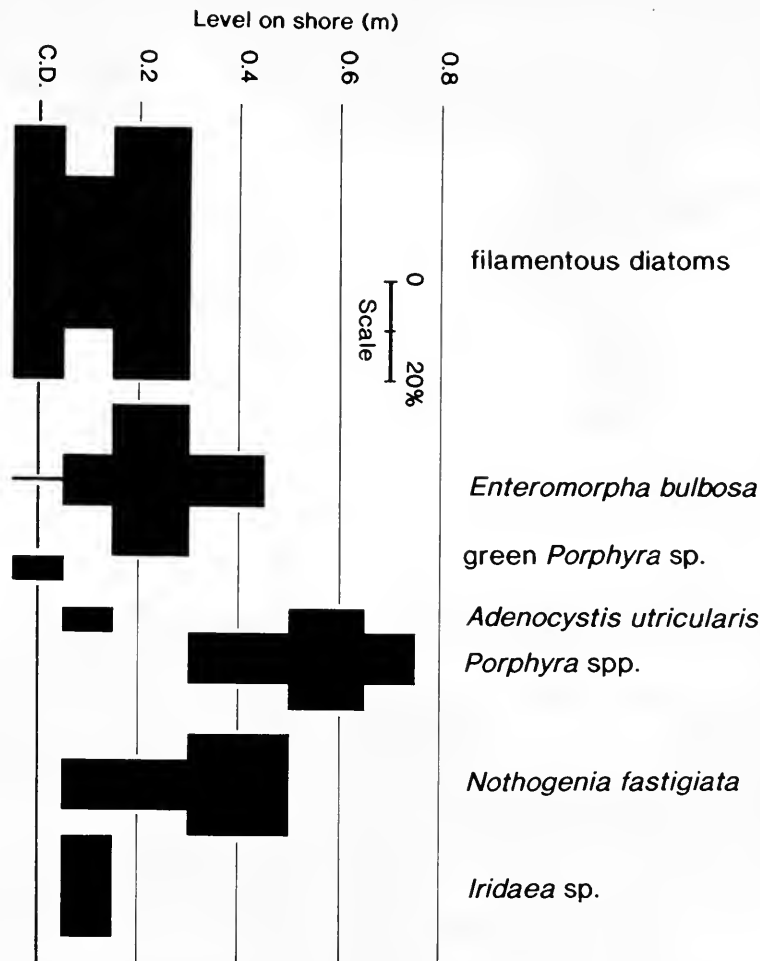


Fig. 6 The vertical distribution and percentage cover abundance of seaweeds on the boulder shore transect D.

Prasiola filiformis Reinsch var. **minuta** Reinsch

Status of this taxon requires investigation.

Ulothrix sp.

Reported as *Hormiscia parasitica*.

According to Papenfuss (1964: 1), this record is 'probably representative of one of the species of *Ulothrix* that has been reported from Antarctica'.

Ulva lactuca Linnaeus var. **macrogyna** Reinsch

Status of this taxon requires investigation.

Phaeophyta

Adenocystis utricularis (Bory de Saint-Vincent) Skottsberg

Recorded as *Chroa sacculiformis*.

Ascoseira mirabilis Skottsberg

Reported as *Lessonia fuscescens* var. *linearis*.

Caepidium antarcticum J. Agardh

Cladothele decaisnei Hooker f. & Harvey

Recorded as *Stictosiphon decaisnei*.

Corycus lanceolatus (Kuetzing) Skottsberg

Recorded as *C. prolifer*.

Desmarestia antarctica Moe & Silva

South Georgia is its northernmost limit of distribution. Its minute gametophytic stage is endophytic on *Cordiaea recovitzae* (see Moe &

Silva, 1989), a red alga also at the limit of its range.

Desmarestia ligulata (Lightfoot) Lamouroux

Recorded as *D. firma*.

Desmarestia menziesii J. Agardh

Recorded as *D. aculeata* var. *compressa*, *D. compressa* and *D. harveyana*.

Desmarestia pteridoides Reinsch

Status of this plant remains uncertain, see remarks in Skottsberg (1907: 20).

Desmarestia willii Reinsch

This southern hemisphere species is closely related to *D. viridis* known only from the northern hemisphere. According to Ricker (1987: 126), the southern hemisphere species shows wide variation in key characters and so is less distinct than Reinsch (1888: 191) indicated when justifying its creation.

Durvillaea antarctica (Chamisso) Hariot

Ectocarpus constanciae Hariot

Ricker (1987: 67) separates it from *E. siliculosus* upon its greater cell diameters, tapering of apical branches, absence of hook-shaped laterals, presence of fewer corticating rhizoids covering lower axes, helical coiling of ribbon-like plastids, and more elongate and solitary plurangia. He accepts that the two species may form part of the form range continuum of *E. siliculosus*.

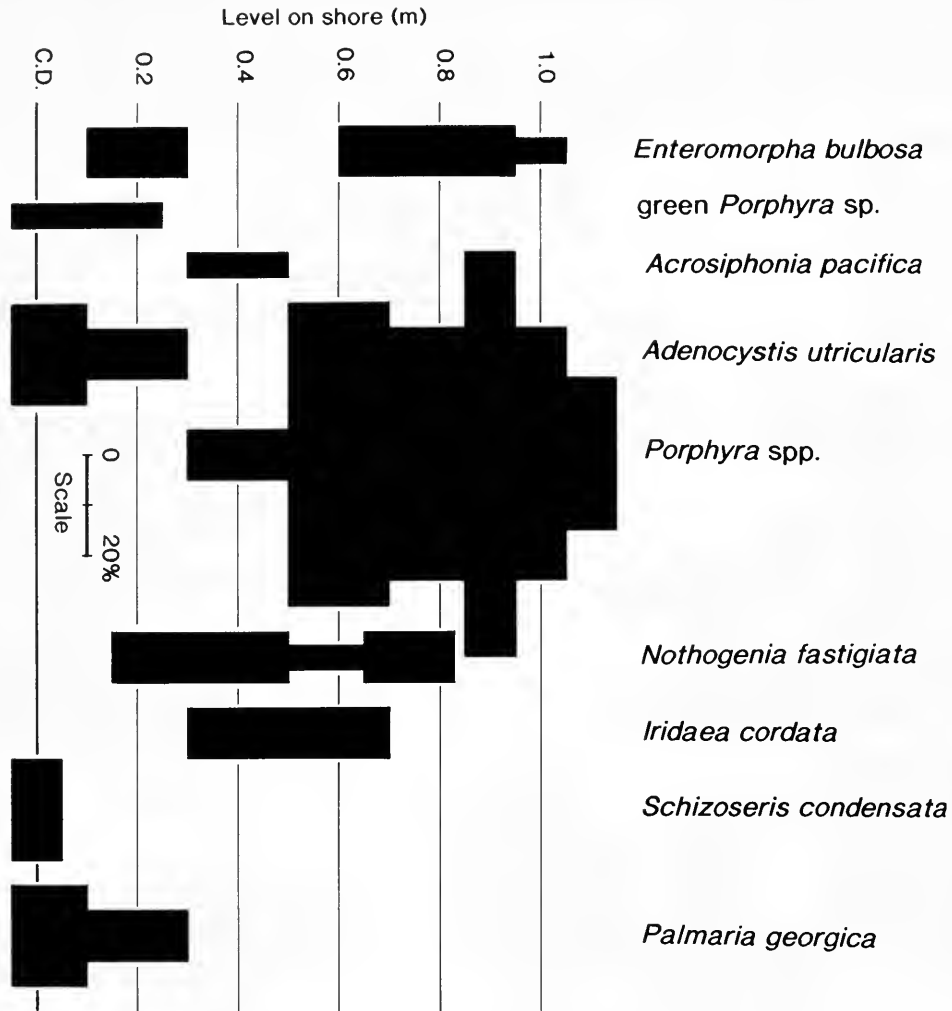


Fig. 7 The vertical distribution and percentage cover abundance of seaweeds on the boulder shore transect E.

Ectocarpus exiguus Skottsberg

Recorded as *E. humilis*.

Ectocarpus siliculosus (Dillwyn) Lyngbye

Recorded as *E. confervoides* and *E. fasciculatus*.

Elachista meridionalis Skottsberg

Geminocarpus austrogeorgiae Skottsberg

Geminocarpus geminatus (Hooker f. & Harvey) Skottsberg

Recorded as *Ectocarpus geminatus*.

Halopteris funicularis (Montagne) Sauvageau

Recorded in table (Skottsberg, 1941: 76) showing Antarctic distribution of algae. No indication given as to source and not mentioned in Papenfuss's (1964) catalogue of Antarctic and sub-Antarctic algae.

Halopteris obovata (Hooker f. & Harvey) Sauvageau

Himantothallus grandifolius (A. & E.S. Gepp) Zinova

Recorded as *Laminaria saccharina* var. *angustata*, *Himantothallus spiralis* and *Phyllogigas grandifolius*.

Lessonia fuscescens Bory

Recorded as *L. flavicans*.

It seems very likely that this large brown alga, characteristic of many sub-Antarctic shores, grows attached on South Georgia despite Skottsberg's (1921) statement (p. 47) that 'Drifted pieces have been

observed along the coast of S. Georgia where according to my impression this plant does not grow'.

Macrocystis pyrifer (Linnaeus) C. Agardh

Recorded as *M. pyrifer* var. *longibullata*.

Melastictis desmarestiae Reinsch

Status of this monotypic genus is uncertain.

Myrionema densum Skottsberg

Myrionema incommodum Skottsberg

Adenocystis the host alga.

Myrionema inconspicuum Reinsch

Very similar to *M. densum* and *M. coronnae*; Skottsberg (1921) suggests *M. inconspicuum* and *M. densum* to be conspecific.

Myrionema macrocarpum Skottsberg

Record from a table showing Antarctic distribution of algae (Skottsberg, 1907). No indication given as to source and Papenfuss (1964) does not mention it from South Georgia.

Myrionema? paradoxum Reinsch

Reinsch's description and illustration of this species and *M. inconspicuum* (Reinsch, 1890) are equivocal, see comments in Ricker (1987: 83).

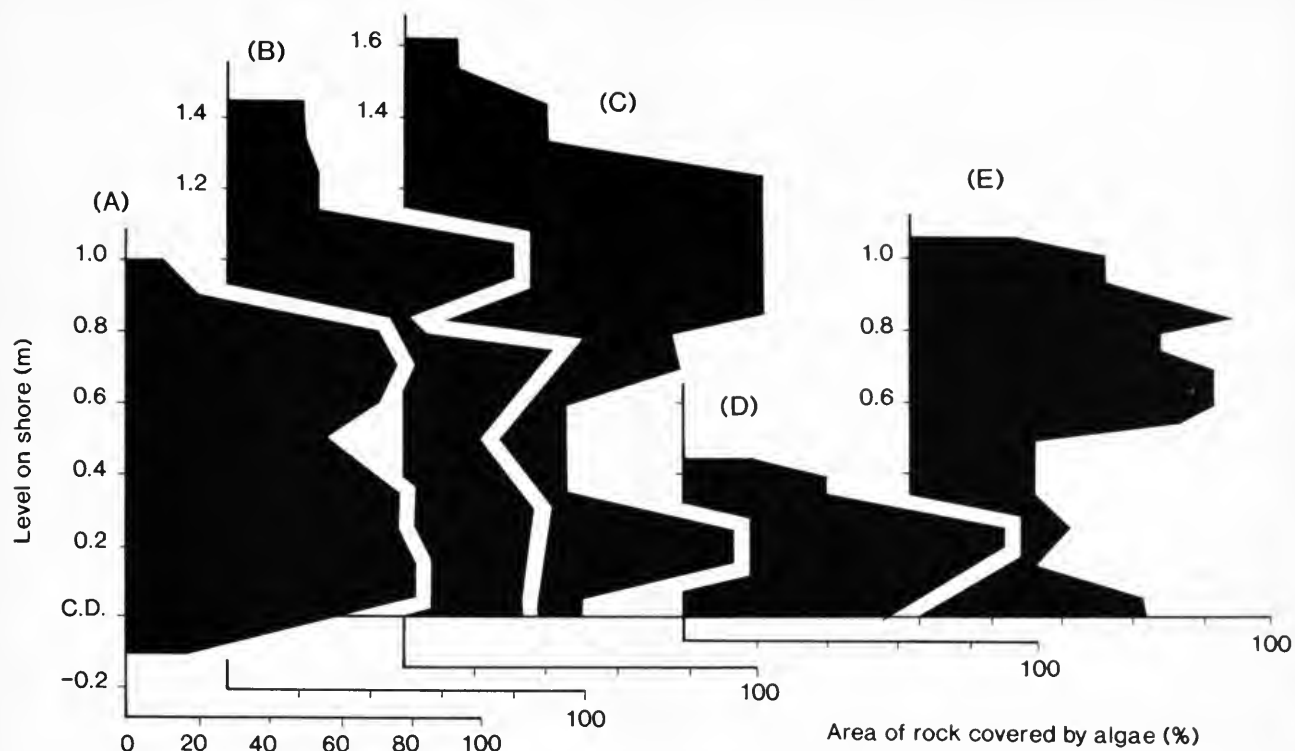


Fig. 8 Total percentage cover abundance of seaweeds at different levels on each of the five shore transects.

Petalonia fascia (O.F. Mueller) Kuntze
Recorded as *Phyllitis fascia* and *Ilea fascia*.

Petroderma maculiforme (Wollny) Kuckuck

Phaearthron austrogeorgica (Skottsberg) Pedersen
Recorded as *Xanthosiphonia austrogeorgica*.

Pilayella littoralis (Linnaeus) Kjellman
Recorded as *Pylaiella opposita*.

Scytosiphon lomentaria (Lyngbye) Link

Scytothamnus fasciculatus (Hooker f. & Harvey) Cotton
Recorded as *S. australis*.

Stegastrum porphyrae Reinsch
Status of this monotypic genus is uncertain.

Syringoderma australe Levring

Utriculidium durvillaei (Bory) Skottsberg
Morphologically very similar to *Adenocystis utricularis*. Differs in the cortical cells possessing a single (not several) plastid and only plurilocular sporangia known. Some authors have suggested that they are alternate phases of a single species.

Rhodophyta

Ahnfeltia plicata (Hudson) Fries

Anisocladella serratodentata (Skottsberg) Skottsberg
Recorded as *Delesseria erratodentata*.

Antithamnion ptilota (Hooker f. & Harvey) Gibson
Ricker (1987: 240) examined the type (*Callithamnion ptilota* Hooker f. & Harvey, 1845) and concluded that it 'may be identical to *D[asyptilon]. pellucidum*, as both species have similar apical development and branching patterns'. He left unresolved the question of conspecificity since no reproductive structures were present on the

type. If they should prove to be conspecific then the correct epithet for the species will be *Dasyptilon ptilota*.

Ballia callitricha (C. Agardh) Kuetzing

Bostrychia vaga Hooker f. & Harvey

?**Calliblepharis ciliata** (Hudson) Kuetzing
Recorded as *Rhodymenia ciliata* var. *ligulata*.
The identity of this plant remains uncertain.

Callithamnion montagnei Hooker

A new record for South Georgia and deposited in the Herbarium in the Department of Botany, The Natural History Museum, London. It was discovered as one of three red algae (*Ceramium rubrum*, *Plocamium secundatum*) entangled with or growing epiphytically on a specimen of *Phycodrys quercifolia* collected from Possession Bay in January 1867 by Dr R.O. Cunningham.

?**Callonema olivaceum** Reinsch

The identity of this taxon remains uncertain (Papenfuss, 1964).

?**Callophyllis cristata** (C. Agardh) Kuetzing

Recorded as *Euthora cristata* and *Rhodymenia cristata*.
A questionable determination according to Skottsberg (1941).

Callophyllis linguata Kytlin

Callophyllis variegata (Bory de Saint Vincent) Kuetzing
Recorded as *Kallymenia multifida* and *Callymenia multifida*.

Ceramium diaphanum (Lightfoot) Roth

Ceramium involutum Kuetzing

Ceramium rubrum (Hudson) C. Agardh

?**Choreocolax rhodymeniae** Reinsch

Parasitic alga on *Palmaria*.
The identity of this species remains uncertain.

Cladodonta lyallii (Hooker f. & Harvey) Skottsberg

A new record for South Georgia based on three specimens in the Herbarium in the Department of Botany, The Natural History Museum, London. Material collected in January 1867 by Dr R.O. Cunningham from Possession Bay during the extra-tropical South America survey of H.M.S. Nassau.

Clathromorphum obtectulum (Foslie) Adey

Recorded as *Lithophyllum aequabile*, *L. discoideum* f. *aequabilis* and *Antarcticophyllum aequabile*.

Colocodasya inconspicua (Reinsch) Schmitz

Recorded as *Polysiphonia inconspicua* and *Merenia inconspicua*. Parasitic on *Heterosiphonia*.

Curdia recovitzae Hariot ex Wildemann

Recorded as *Kallymenia reniformis* f. *carcosa* and *Callymenia reniformis*.

Delesseria salicifolia Reinsch

Indistinguishable on vegetative features from *D. lancifolia*, but separated on form of the cystocarp and specialized sporophylls containing tetrasporangia.

Delisea pulchra (Greville) Montagne

Recorded as *Bonnemaisionia prolifera*.

Falklandiella harveyi (Hooker f.) Kylin

Recorded as *Dasyptylon harveyi*, *Plumaria harveyi* and *Euptilota harveyi*.

For discussion of distinctions between this genus and others including *Dasyptylon*, see Moe & Silva (1979).

Georgiella confluens (Reinsch) Kylin

Recorded as *Ptilota confluens*, *Euptilota confluens* and *Plumariopsis eatoni*.

This genus and *Plumariopsis* are endemic to the southern hemisphere and are morphologically similar. Moe & Silva (1983) tabulate a number of vegetative and reproductive features that distinguish them.

Heterosiphonia berkeleyi Montagne

Recorded as *Merenia microcladioides* and *Heterosiphonia merenia*.

Hydrolithon discoideum (Foslie) Mendoza & Cabioch

Recorded as *Lithophyllum discoideum*, *Pseudolithophyllum discoideum* and *Spongites discoidea*.

?Hymenocladopsis crustigena Moe

Recorded as *Gracilaria prolifera*.

Doubt concerns the exact status of the South Georgian material. Moe (1986) has investigated the type of *Gracilaria prolifera* and states that it is 'certainly placed incorrectly as to genus .. Although nothing precludes its assignment to *Hymenocladopsis*, I hesitate to propose a new combination without seeing tetrasporangial material or material in which the presence or absence of gland cells can be determined with certainty. It is possible that the plants from the Antarctic Peninsula on which the new genera is based are conspecific with *Gracilaria prolifera*'. Should this prove to be the case then the epithet '*prolifera*' would have priority.

Iridaea cordata (Turner) Bory de Saint-Vincent

Recorded as *I. micans* and *I. cordata* f. *ligulata* (type locality of trivial growth form).

Leister (1977) regards several earlier described species as conspecific with *I. cordata*.

Iridaea obovata Kuetzing

Recorded as *Iridaea macrodonta* and *Rhodoglossum macrodontum*.

Microrhinus carnosus (Reinsch) Skottsberg

Recorded as *Delesseria carcosa* and *Chauvinia carcosa*.

Mesophyllum schmitzii (Hariot) Mendoza

Recorded as *Lithothamnion schmitzii*.

The original record on which this report is based has not been traced (see Ricker, 1987: 175).

?Myriogramme livida (Hooker f. & Harvey) Kylin

Skottsberg (1941: 76) tabulated the distribution of Antarctic and sub-Antarctic algae. No indication was given as to source and Skottsberg's record was not mentioned by Papenfuss (1964) in his catalogue of Antarctic and sub-Antarctic algae.

Myriogramme smithii (Hooker f. & Harvey) Kylin

Recorded as *Nitophyllum fuscobrunum* and *N. smithii*.

Nereoginkgo adiantifolia Kylin**Neuroglossum ligulatum** (Reinsch) Skottsberg

Recorded as *Delesseria ligulata* and *Choreocolax delesseriae*.

Nothogenia fastigiata (Bory de Saint-Vincent) Parkinson

Recorded as *Chondrus crispus* var. *pigmaeus* and *Chaetangium fastigiatum*.

Palmaria decipiens (Reinsch) R.W. Ricker

Recorded as *Rhodymenia decipiens*, *R. palmata* sensu Reinsch, *R. palmata* var. *multiloba*, *Leptosarca alcornis* and *L. decipiens*.

According to Ricker (1987: 221), it is morphologically very similar to the type species of *Palmaria* (*P. palmata*) but distinguished by the readiness of its tissues to soften in 4% formalin-seawater.

Palmaria georgica (Reinsch) R.W. Ricker

Recorded as *Rhodymenia georgica*, *R. palmatiformis* and *R. palmatiformis* var. *austrogeorgica*.

The overlap in thallus morphology of the two *Palmaria* species has led Ricker (1987: 224) to suggest that *P. georgica* may be 'merely a diminutive form or an ecotype of *P. decipiens*'. *P. georgica* separates from *P. decipiens* by forming tufts composed of many fronds, its bushier form, presence of cortical hairs, and occupying a different habitat.

Pantoneura plocamioides Kylin**Phycodrys austrogeorgica** Skottsberg**Phycodrys quercifolia** (Bory) Skottsberg

Recorded as *Delesseria quercifolia*.

Phyllophora antarctica A. & E.S. Gepp

Recorded as *Ahnfeltia plicata* and *Phyllophora ahnfeltioides*.

Phyllophora appendiculata Skottsberg

According to Skottsberg (1953: 542), this species might be identical with *Gymnogongus turqueti* Hariot (a *Phyllophora*, see Ricker, 1987: 202).

Picconiella plumosa (Kylin) De Toni

Recorded as *Dasya? pectinata* and *Pteronia plumosa*.

?Plectoderma minus Reinsch

Uncertainty surrounds the taxonomic status of this taxon. The genus was established by Reinsch (1874) for two species of simple, crustose coralline algae. According to Chamberlain (1983: 308), this species 'was probably *Melobesia membranacea* judging by the cell shape and general disc pattern . . . No specimens have been found of either species so further identification is not possible'.

Plocamium cartilagineum (Linnaeus) Dixon

Recorded as *P. coccineum*.

Plocamium hookeri Harvey**Plocamium secundatum** (Kuetzing) Kuetzing**Polycoryne radiata** Skottsberg

Parasitic on *Schizoseris dichotoma*.

Polysiphonia anisogona Hooker f. & Harvey**Porphyra endiviifolium** (A. & E.S. Gepp) ChamberlainRecorded as *Monostroma endiviifolium*.

Chamberlain (1963: 152) believed Hylmo's (1919: 6) record from South Georgia was based on a misidentification. New collections from the island now confirm its presence.

Porphyra umbilicalis (Linnaeus) KuetzingRecorded as *P. laciniata* and *Wildemannia laciniata*.**Pseudolaingia larsenii** (Skottsberg) LevringRecorded as *Delesseria larsenii*.**Pterothamnion simile** (Hooker f. & Harvey) NaegeliRecorded as *Callithamnion pinastroides* var. *ramulosum*, *Antithamnion ramulosum* and *A. simile*.**Sarcodia montagneana** (Hooker f. & Harvey) J. Agardh**Schizoseris condensata** (Reinsch) R.W. RickerRecorded as *Delesseria condensata*, *Nitophyllum condensata*, *N. multinerve* pro parte, *N. affine*, *Schizoseris laciniata* and *Delesseria laciniata*.

See Ricker (1987: 285, 286) for discussion of nomenclature and synonymy.

Schizoseris dichotoma (Hooker f. & Harvey) KylinRecorded as *Delesseria polydactyla*, *Myriogramme multinervis*, *Nitophyllum polydactylum* and *Schizoseris polydactyla*.**Synarthrophyton patena** (Hooker f. & Harvey) TownsendRecorded as *Lithothamnium antarcticum*.*Rejected records***Cystosphaera jacquinotii** (Montagne) Skottsberg

South Georgia: Neuschul (1968). Despite mentioning this taxon as occurring at this locality in the text (p. 10), it is not indicated on his distribution map nor the source of the record given (see Lamb & Zimmerman, 1977: 174).

Plumariopsis eatoni (Dickie) De ToniThe report of this taxon from South Georgia by Kylin & Skottsberg (1919) is probably a misdetermination for the closely related **Georgiella confluens** (see above). Moe & Silva (1983) believe this species does not occur in Antarctica despite earlier reports.

DISCUSSION

Shore ecology

The upper part of the eulittoral zone of rocky shores within Husvik Harbour is dominated by belts of *Porphyra* or mixed belts of *Porphyra/Nothogenia*. Similar belts were described by Skottsberg (1941) at this shore level at May Cove (=Mauviken), Cumberland Bay where an 'Adenocystis-Chlorophyceae association' was observed on the lower shore. Skottsberg makes no reference to belts of *Schizoseris* or *Palmaria*, but simply mentions that these two red algae were largely confined to tide pools containing a reasonably diverse algal community. He reported a '*Rhodymenia* [= *Palmaria*]-*Lithophyllum* association' in rock-lined pools and a '*Rhodymenia* [= *Palmaria*] association' in stony pools, while brackish-water pools contained *Adenocystis*, *Scytosiphon*, and *Utriculidium*. In the present study green algae were frequent in the littoral zone although the two most abundant taxa (*Enteromorpha*, *Acrosiphonia*) did not form a distinctive

belt. Only on boulder shores were green algae found to be relatively abundant. On one of the rocky shores a coating of a green filamentous alga was observed in the upper eulittoral zone (probably *Ulothrix*; not collected). No mention is made by Skottsberg (1941) of any green algae in his study of a stony beach at Boiler Bay (=Grytviken), Cumberland Bay where algal diversity was considerably less compared to the boulder shores studied at Husvik Harbour where *Adenocystis* and *Nothogenia* ('*Adenocystis-Chaetangium* [= *Nothogenia*] association') dominated. Unlike Husvik Harbour, the shores in Grytviken are affected by small icebergs ('growlers') produced by calving glaciers of which seven occur in the Cumberland Bay complex. Ice-scour and abrasion are known to be major physical factors affecting sessile shore organisms in high latitudes (see Keats et al., 1985).

Our observations on the distribution of shore algae show close agreement with many of those made by Skottsberg (1941) in the early years of this century. He was of the opinion that his general observations enabled him to have a 'fair idea of the composition of the vegetation [algae]' of South Georgia. Of the 21 stations described by Skottsberg, all were relatively sheltered and confined to north-easterly shores. If he had been as familiar with South Georgia as claimed then it is surprising that he overlooked the bull kelp *Durvillaea antarctica*, first reported by Will in 1890 and yet going unmentioned by Reinsch (1888, 1890) who determined his algal material. Will's report of *Durvillaea* growing on rocky headlands on South Georgia was confirmed by Hay (1988, based on personal observations by Knowles) who states it forms (p. 426) 'a distinctive band in the low intertidal zone on the outer coast between Cumberland Bay and Royal Bay'. In 1991 one of us (PJAP) found a large bed of *Durvillaea* growing in the sublittoral fringe at Tonsberg Point (see Fig. 1). A large proportion of the tidal drift within Husvik Harbour comprises *Durvillaea*, much of it probably originates from this Point. On wave-exposed coasts *Durvillaea antarctica* characterizes the sublittoral fringe as reported on other sub-Antarctic shores (see Stephenson & Stephenson, 1972).

The general distribution pattern of shore algae described on South Georgia during the short austral summer resembles those of sub-Antarctic and Antarctic rocky shores so far investigated (Knox, 1960; Kenny & Haysom, 1962; Price & Redfearn, 1968; Smith & Simpson, 1985; Delepine et al., 1966; Stephenson & Stephenson, 1972, among others). Absent from the littoral fringe are macroscopic growths of algae and the upper eulittoral subzone is defined by the genus *Porphyra*, below which appears *Nothogenia*. Simpson (1976) used the upper limit of *Porphyra* to define the upper limit of the eulittoral zone on Macquarie Island. Most algae on the lower shore seem confined to pools with the exception of *Adenocystis*, *Iridaea*, *Schizoseris* and *Palmaria*. As mentioned above, these algae are present in the lower eulittoral zone and are common at this level on other shores of the Southern Ocean (see Stephenson & Stephenson, 1972). Calcareous coralline algae or 'lithothamnia', often characteristic of the lower eulittoral subzone on lower latitude shores, form evident crusts in the sublittoral fringe on South Georgia. These crusts correspond to the '*Lithophyllum-Lithothamnion* association' of Antarctic shores, an association typically confined to rock pools and whose upper limit indicates the mean low tide level on sloping rocky shores (see Delepine et al., 1966). The presence of a '*Hildenbrandia*' or '*Hildenbrandia-Bostrychia* association' on several sub-Antarctic shores has

not been observed on South Georgia.

The sublittoral fringe on South Georgia is defined by the upper distributional limit of two kelps: juveniles of *Macrocystis pyrifera* on sheltered to moderately wave-exposed shores, and mature plants of *Durvillaea antarctica* on wave-exposed headlands. These brown algae characterize this fringe on sub-Antarctic and cold temperate shores, both reaching the southernmost limit of their distribution in South Georgia and Tierra del Fuego. The presence of *Macrocystis* on South Georgia led Skottsberg (1941) to remark (p. 36) that 'from the very first the visitor gets the impression that, regarded from an algological viewpoint, South Georgia must be included in the Subantarctic zone'. This statement was made at a time when Skottsberg had rejected *Durvillaea antarctica* as indigenous to the island.

The high diversity and biomass of subtidal algal vegetation markedly contrasts with the low diversity and comparative barrenness of the littoral zone. On rocky bottoms the large kelps are the canopy dominants. In the entrance to sheltered inlets such as Grytviken (=Boiler Bay), a '*Macrocystis-Desmarestia-Pteronia-Plocanium* association' was reported by Skottsberg (1941) as growing on stones down to a depth of 25 m. He noted that some of the dominant lower littoral algae (e.g. *Palmaria* sp. [as *Rhodymenia palmatiformis*]) grew to a depth as great as 30 m and described a number of associations which, albeit sampled indirectly by trawling, seemed to vary according to depth and substratum type.

Marine algal flora

The South Georgian algal flora is surprisingly diverse (103 species, 75 genera) considering the few shores (mostly wave-sheltered) investigated on its north-eastern coast during just a few austral summers. Undoubtedly species records for the island would increase if wave-exposed shores were visited and more subtidal collecting was undertaken. Skottsberg (1964), in recalling his two summers on South Georgia, states (p. 149) 'my journal from 1902-03 contains rough drawings of unknown Rhodophyceae lost in the shipwreck and never collected a second time'.

Of the 103 species of marine algae known from South Georgia, nine are green algae, 35 brown algae, and two of the 47 red algae are unpublished records (*Cladodonta lyallii*, *Callithamnion montagnei*). The island is the type locality for 32 species (four genera), and yet South Georgia has just four endemic species and one endemic genus (Tables 1, 2). The taxonomic status of these endemics and endemic infraspecific taxa (*Iridaea cordata* f. *ligulata*, *Prasiola filiformis* var. *minuta*, *Ulva lactuca* var. *macrogyra*) is questionable. Twelve algal species are known only from South Georgia and Tierra del Fuego (Kuhnemann, 1972), an island lying about 2150 km due west of it. About 22% of the South Georgian algae also occur in the Northern Hemisphere, while *Etonema tenuissimum*, *Calliblepharis ciliata*, *Callonema olivaceum* and *Callophyllis cristata* are only known in the Southern Hemisphere from this island; all four records are regarded as doubtful. Almost half of its species are known from the Antarctic, the remainder reach their southernmost limit within the sub-Antarctic region. About 47% of the South Georgian marine algae are known from sub-Antarctic islands at similar or more northerly latitudes and mainland South America (see Tables 1, 2). The remainder are confined to more southerly latitudes with a few reaching their northernmost limit at South Georgia (e.g. *Desmarestia antarctica*).

Table 1 An analysis of the marine benthic algae of South Georgia.

	Distribution					
	A	s-A	SG only	SG+TF only	NH	SG type loc.
<i>Acrosiphonia pacifica</i>	+	+	-	-	+	-
<i>Adenocystis utricularis</i>	+	+	-	-	-	-
<i>Ahnfeltia plicata</i>	+	+	-	-	+	-
<i>Anisocladella serratodentata</i>	-	+	-	+	-	+
<i>Antithamnion pilota</i>	-	+	-	-	-	-
<i>Ascoseira mirabilis</i>	+	+	-	-	-	+
<i>Ballia callitricha</i>	+	+	-	-	-	-
<i>Bostrychia vaga</i>	-	+	-	-	-	-
<i>Caepidium antarcticum</i>	-	+	-	-	-	-
? <i>Calliblepharis ciliata</i>	-	+	-	-	+	-
<i>Callithamnion montagnei</i>	-	+	-	-	-	-
? <i>Callonema olivaceum</i>	-	+	-	-	+	-
? <i>Callophyllis cristata</i>	-	+	-	-	+	-
<i>Callophyllis linguata</i>	-	+	-	+	-	+
<i>Callophyllis variegata</i>	+	+	-	-	+	-
<i>Ceramium diaphanum</i>	-	+	-	-	+	-
<i>Ceramium involutum</i>	+	+	-	-	-	-
<i>Ceramium rubrum</i>	-	+	-	-	+	-
? <i>Choreocolax rhodymeniae</i>	-	+	-	+	-	+
<i>Cladodonta lyallii</i>	-	+	-	-	-	-
<i>Cladophora incompta</i>	-	+	-	-	-	-
<i>Cladothele decaisnei</i>	-	+	-	-	-	-
<i>Clathromorphum obtectulum</i>	-	+	-	-	-	-
<i>Colacodasya inconspicua</i>	-	+	-	-	+	-
<i>Corycus lanceolatus</i>	-	+	-	-	-	-
<i>Curdiea recovitzae</i>	+	+	-	-	-	-
<i>Delesseria salicifolia</i>	-	+	-	-	-	+
<i>Delisea pulchra</i>	+	+	-	-	-	-
<i>Desmarestia antarctica</i>	+	+	-	-	-	-
<i>Desmarestia ligulata</i>	-	+	-	-	+	-
<i>Desmarestia menziesii</i>	+	+	-	-	-	-
<i>Desmarestia pteridoides</i>	-	+	-	+	-	+
<i>Desmarestia willii</i>	+	+	-	-	-	-
<i>Durvillaea antarctica</i>	+	+	-	-	-	-
<i>Ectocarpus constanciae</i>	-	+	-	-	-	-
<i>Ectocarpus exiguus</i>	-	+	-	+	-	-
<i>Ectocarpus siliculosus</i>	-	+	-	-	+	-
<i>Elachista meridionalis</i>	-	+	-	+	+	-
<i>Enteromorpha bulbosa</i>	+	+	-	-	-	-
<i>Enteromorpha gunniana</i>	+	+	-	-	-	-
<i>Etonema subcorticale</i>	-	+	+	-	-	+
<i>Etonema tenuissimum</i>	-	+	-	-	+	-
<i>Falklandiella harveyi</i>	-	+	-	-	-	-
<i>Geminocarpus austrogeorgiae</i>	+	+	-	-	-	+
<i>Geminocarpus geminatus</i>	+	+	-	-	-	+
<i>Georgiella confluens</i>	+	+	-	-	+	-
<i>Halopteris funicularis</i>	-	+	-	-	-	-
<i>Halopteris obovata</i>	-	+	-	-	-	-
<i>Heterosiphonia berkeleyi</i>	+	+	-	-	-	-
<i>Himantothallus grandifolius</i>	+	+	-	-	-	-
<i>Hydrolithon discoideum</i>	-	+	-	-	-	-
? <i>Hymenocladopsis crustigena</i>	+	+	-	-	-	-
<i>Iridaea cordata</i> (form)	+	+	-	-	-	-
<i>Iridaea obovata</i>	+	+	-	-	+	-
<i>Lessonia fuscescens</i>	-	+	-	-	-	-
<i>Macrocystis pyrifera</i>	-	+	-	-	+	-
<i>Melastictis desmarestiae</i>	-	+	+	-	-	+
<i>Mesophyllum schmitzii</i>	+	+	-	-	-	-
<i>Microrhinus carnosus</i>	-	+	-	+	-	+
? <i>Myriogramme livida</i>	-	+	-	-	-	-
<i>Myriogramme smithii</i>	+	+	-	-	-	-
<i>Myrionema densum</i>	-	+	-	-	-	-
<i>Myrionema incommodum</i>	+	+	-	-	-	+
<i>Myrionema inconspicuum</i>	-	+	-	+	-	+

Table 1 cont.

	Distribution					
	A	s-A	SG only	SG+TF only	NH	SG type loc.
<i>Myrionema macrocarpum</i>	-	+	-	-	-	-
<i>Myrionema paradoxum</i>	-	+	-	+	-	+
<i>Nereoginkgo adiantifolia</i>	+	+	-	-	-	-
<i>Neuroglossum ligulatum</i>	-	+	-	+	-	+
<i>Nothogenia fastigiata</i>	-	+	-	-	-	-
<i>Palmaria decipiens</i>	+	+	-	-	-	+
<i>Palmaria georgica</i>	+	+	-	-	-	+
<i>Pantoneura plocamioides</i>	+	+	-	-	-	+
<i>Petalonia fascia</i>	-	+	-	-	+	-
<i>Petroderma maculiforme</i>	+	+	-	-	+	-
<i>Phaeothron austrogeorgica</i>	-	+	-	+	-	+
<i>Phycodrys austrogeorgica</i>	-	+	-	+	-	+
<i>Phycodrys quercifolia</i>	+	+	-	-	-	-
<i>Phyllophora antarctica</i>	+	+	-	-	-	-
<i>Phyllophora appendiculata</i>	+	+	-	-	-	+
<i>Picconella plumosa</i>	+	+	-	-	-	-
<i>Pilayella littoralis</i>	+	+	-	-	+	-
? <i>Plectoderma minus</i>	-	+	+	-	-	+
<i>Plocamium cartilagineum</i>	+	+	-	-	+	-
<i>Plocamium hookeri</i>	+	+	-	-	-	-
<i>Plocamium secundatum</i>	+	+	-	-	-	-
<i>Polycoryne radiata</i>	-	+	-	-	-	+
<i>Polysiphonia anisogona</i>	-	+	-	-	-	-
<i>Porphyra endiviifolium</i>	+	+	-	-	-	-
<i>Porphyra umbilicalis</i>	+	+	-	-	+	-
? <i>Prasiola crista</i>	+	+	-	-	+	-
(subsp. antarctica)						
<i>Prasiola filiformis</i>	-	+	-	-	-	-
(var. minuta)						
<i>Pseudolaingia larsenii</i>	-	+	-	-	-	+
<i>Pterothamnion simile</i>	+	+	-	-	-	-
<i>Sarcodia montagneana</i>	-	+	-	-	-	+
<i>Schizoseris condensata</i>	-	+	-	-	-	+
<i>Schizoseris dichotoma</i>	-	+	-	-	-	-
<i>Scytosiphon lomentaria</i>	-	+	-	-	+	-
<i>Scytothamnus fasciculatus</i>	+	+	-	-	-	-
<i>Stegastrum porphyrae</i>	-	+	+	-	-	+
<i>Synarthrophyton patena</i>	+	+	-	-	-	-
<i>Syringoderma australe</i>	+	+	-	-	-	+
<i>Ulva lactuca</i>	-	+	-	-	+	-
(var. macrogyna)						
<i>Utriculidium durvillaei</i>	+	+	-	-	-	-

Key to abbreviations: A, Antarctic (latitudes <55° S); s-A, sub-Antarctic; SG, South Georgia; TF, Tierra del Fuego; NH, Northern Hemisphere.

A recent ordination analysis of the algal floras of the Southern Oceans by John et al. (1994) supports the findings of Lawson (1988: fig. 7) and Ricker (1987) who contend that the sub-Antarctic region represents a single circumpolar province. They observed no sharp discontinuity between the algal floras of the Antarctic and sub-Antarctic despite the principal surface water currents running counter to one another in the two regions. The close similarity between different sub-Antarctic islands is remarkable considering the remoteness and often vast distances separating many of them. It is speculated that much of the sub-Antarctic flora results from the long distance dispersal by the West Wind Drift of plants originating on South American shores.

In conclusion, further investigations are required to determine just how typical are the distribution patterns of algae in

Table 2 Summary of an analysis of the marine benthic algae of South Georgia.

	Distribution					
	A	s-A	SG only	SG+TF only	NH	SG type loc.
Chlorophyta	4	5	1	0	4	1
Phaeophyta	14	21	2	6	7	13
Rhodophyta	29	28	1	6	11	18
TOTAL	47	54	4	12	22	32

Key to abbreviations: A, Antarctic (latitudes <55° S); s-A, sub-Antarctic region; SG, South Georgia; TF, Tierra del Fuego; NH, Northern Hemisphere.

Husvik Harbour compared to other South Georgian shores. Advances in our knowledge of the seaweeds of South Georgia and the Southern Ocean in general continue to be hampered by lack of material (especially collected by SCUBA diving), paucity of taxonomic research on new or historically-important collections, absence of seasonal observation on shore algae and few experimental studies designed to provide information on dynamics including plant-animal interactions.

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Studies in *Pseudocyphellaria* (Lichens) IV*. Palaeotropical species (excluding Australia)

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SYNOPSIS. Twenty-nine species of *Pseudocyphellaria* are recorded from the palaeotropics (from Africa to the eastern Pacific but excluding Australia) viz., *P. argyracea*, *P. aurata*, *P. beccarii*, *P. carpoloma*, *P. clathrata*, *P. crocata*, *P. crocatoides*, *P. desfontainii*, *P. dissimilis*, *P. dozyana*, *P. gilva*, *P. godeffroyii*, *P. haywardiorum*, *P. homalosticta*, *P. insculpta*, *P. intricata*, *P. maculata*, *P. multifida*, *P. neglecta*, *P. pickeringii*, *P. poculifera*, *P. prolificans*, *P. punctularis*, *P. reineckeana*, *P. rigida*, *P. semilanata*, *P. stenophylla*, *P. sulphurea* and *P. trichophora*. Details of their anatomy, chemistry, morphology and distribution are presented together with a key. The following new combinations are proposed: *P. beccarii* (Kremp.) D.J. Galloway and *P. trichophora* (Vain.) D.J. Galloway.

INTRODUCTION

Species of *Pseudocyphellaria* are conspicuous, leafy, foliose lichens best developed and with richest biodiversity in rainforest, shrubland and successional vegetation, or subalpine and alpine grassland habitats of the Southern Hemisphere cool temperate zone, with major areas of speciation being New Zealand (Galloway, 1988) and southern South America (Galloway, 1992). In tropical regions *Pseudocyphellaria* is most commonly found in montane or mossy cloudforest between 1600 and 3600 m (see discussion on altitudinal zonation in Sipman (1993)), but several widespread species such as *P. aurata*, *P. crocata* and *P. intricata* occur at lower altitudes and in lowland and coastal sites as well. The contribution of species of *Pseudocyphellaria* to the 'Lobarion' alliance in south-east Asian forests is discussed in Wolseley (1991).

During a study of Australian species of *Pseudocyphellaria* (in preparation) very many collections from neighbouring areas in the Pacific Basin were examined, so that it is now possible to present a preliminary revision of palaeotropical species. Neotropical taxa in *Pseudocyphellaria* are discussed in accounts of Ecuadorian (Galloway & Arvidsson, 1990) and Brazilian (Galloway, 1993) collections, and in catalogues of Central American (Imshaug, 1956a), Mexican (Imshaug, 1956b) and West Indian (Imshaug, 1957) lichens. Earlier accounts discussing or listing palaeotropical taxa referable to *Pseudocyphellaria* include: Montagne (1856), Krempelhuber (1875), Zahlbruckner (1908, 1943), Vainio (1913, 1924), Magnusson (1940), Zahlbruckner & Mattick (1956), Szatala (1956), Joshi & Awasthi (1982), Hawksworth & Shaw (1984), Streimann (1986) and Swinscow & Krog (1988).

The context of palaeotropics used in the present account refers to all land in the tropical-subtropical zone outside of the neotropical region, viz., from Africa to the eastern Pacific bordering North, Central and South America and lying roughly between the tropics of Cancer and Capricorn at latitudes 35° north and south of the equator.

Species of *Pseudocyphellaria* discussed in this revision are

generally conspicuous lichens, some often reaching a great size and being among the largest and most rapidly growing of foliose lichens. They grow on twigs, bark, soil, or rock, often over or intermingled with bryophytes or other lichens in a wide variety of habitats. Since all taxa contain cyanobacteria either as a primary photobiont or as internal cephalodia they are efficient nitrogen fixers and important contributors to rainforest nitrogen budgets, a role which is of importance in the maintenance of rainforest biodiversity (Galloway, 1994). Detailed accounts of anatomical, morphological and chemical characters useful in species delimitation in the genus are given in Galloway (1988, 1992) and are not repeated here. The importance and possible role of triterpenoids in *Pseudocyphellaria* are discussed by Galloway (1991) and Wilkins (1993).

The undoubted importance of species of *Pseudocyphellaria* in a variety of tropical ecosystems makes a modern account of this genus a vital necessity. However, in offering this present revision as a contribution to tropical lichenology I must admit to its being almost entirely a herbarium study. I have collected only briefly from Peninsular Malaysia in the palaeotropics and consequently have not had the advantage of assessing variation in the field. Accordingly, I have taken a rather broad view of the limits of taxa and in widespread species, such as *P. argyracea*, *P. crocata*, *P. gilva*, *P. intricata* and *P. sulphurea* for example, I accept a wide morphological variation which seems acceptable based on the variation of these taxa in temperate habitats. It is hoped that the present revision will form a working baseline to the genus in the tropics and encourage lichenologists to undertake closer regional studies of it.

Type and other material was obtained from or examined in the following herbaria: AK, B, BM, BR, BSIP, CBG, COLO, E, G, GB, H, H-ACH, H-NYL, KEP, KLU, L, LD, LG, M, MEL, NY, PC, PC-LENORMAND, PC-THURET, S, TNS, TUR-VAINIO, UKMB, UPS, UPS-THUNBERG, UPSV, US, W, WU and from the following private herbaria: Dr A. Aptroot (Baarn), Dr L. Arvidsson (Göteborg), Prof. G. Degelius (Askim) [Prof. Degelius's lichens are now at UPS], Dr P. Diederich (Luxembourg), Dr K. Kalb (Neu-markt), and Prof. C.W. Smith (Honolulu).

* Part III In *Bibliotheca Lichenologica* 46: 1–275 (1992).

SYSTEMATIC TREATMENT

Key to palaeotropical species of *Pseudocyphellaria*

- 1 Medulla white 2
 Medulla yellow 26
- 2 Photobiont green 3
 Photobiont blue-green 9
- 3 Pseudocyphellae white 4
 Pseudocyphellae yellow 4. *P. carpoloma*
- 4 Pseudocyphellae present on upper surface 5
 Pseudocyphellae not present on upper surface 6
- 5 Isidiate-phyllidiate 15. *P. homalosticta*
 Without isidia or phyllidia 24. *P. reineckeana*
- 6 Without isidia or lobules 7
 Isidiate/lobulate 8
- 7 Lobes broad, punctate-impressed 28. *P. sulphurea*
 Lobes narrow 27. *P. stenophylla*
- 8 Lobes broad, rounded, phyllidiate 18. *P. multifida*
 Lobes narrow, punctate-impressed 22. *P. prolificans*
- 9 Pseudocyphellae white 10
 Pseudocyphellae yellow 21
- 10 With soredia or isidia 11
 Without soredia or isidia 16
- 11 Sorediate 12
 Isidiate/phyllidiate 15
- 12 Upper surface smooth or punctate-impressed; 2 hopanes present 13
 Upper surface faveolate or punctate-impressed; hopane triol present 11. *P. dozyana*
- 13 Upper surface plane or undulate; pseudocyphellae on lower surface rare or absent 16. *P. intricata*
 Upper surface punctate-impressed; pseudocyphellae on lower surface prominent 14. *P. haywardiorum*
- 14 Isidiate 14
 Phyllidiate 9. *P. insculpta*
- 15 Isidia associated with pseudocyphellae 1. *P. argyracea*
 Isidia not associated with pseudocyphellae 10. *P. dissimilis*
- 16 Pseudocyphellae present on upper surface 17
 Pseudocyphellae absent on upper surface 3. *P. beccarii*
- 17 Isidia absent 18
 Isidia or marginal lobules present 23. *P. punctillaris*
- 18 Upper surface plane 19
 Upper surface scrobiculate 25. *P. rigida*
- 19 Upper surface smooth, not areolate-scabrid 20
 Upper surface areolate-scabrid 13. *P. godeffroyii*
- 20 Margins of lobes tomentose-hairy 29. *P. trichophora*
 Margins of lobes glabrous 26. *P. semilanata*
- 21 Sorediate or isidiate/phyllidiate 22
 Without soredia or isidia 25
- 22 Isidiate/phyllidiate 23
 Sorediate 6. *P. crocata*
- 23 Phyllidiate or with marginal or laminal proliferations 24
 Isidiate 8. *P. desfontainii*
- 24 With laminal and marginal proliferations, not truly phyllidi-

- ate 7. *P. crocatoides*
 Phyllidiate 19. *P. neglecta*
- 25 Upper surface deeply faveolate 17. *P. maculata*
 Upper surface undulate 12. *P. gilva*
- 26 Sorediate or isidiate/phyllidiate 27
 Not sorediate, isidiate or phyllidiate 5. *P. clathrata*
- 27 Sorediate 28
 Isidiate/phyllidiate 20. *P. pickeringii*
- 28 Soralia linear, confluent, labriform 2. *P. aurata*
 Soralia derived from small, marginal, crowded isidia
 21. *P. poculifera*

The species

1. *Pseudocyphellaria argyracea* (Delise) Vain. in *Hedwigia* 37: 35 (1898). *Sticta argyracea* Delise in *Mém. Soc. linn. Normandie* 2: 91 pl.7, fig. 30 (1825). *Stictina argyracea* (Delise) Nyl., *Syn. meth. lich.* 1(2): 334 (1860). *Cyanisticta argyracea* (Delise) Gyeln. in *Reprum Spec. nov. Regni veg.* 29: 2 (1931). Type: Ile de la Réunion. Sur des troncs ou les rochers mousses des hautes régions, ?*Bory de St-Vincent*, ex Herb. Bory (PC-THURET-lectotype (Galloway & James, 1986: 429)).
- Sticta argyracea* var. *sorediifera* Delise in *Mém. Soc. linn. Normandie* 2: 92 pl.7, fig.31 (1825). *Stictina argyracea* var. *sorediifera* (Delise) Nyl., *Syn. meth. lich.* 1(2): 334 (1860). *Pseudocyphellaria argyracea* var. *sorediifera* (Delise) Malme in *Bih. K. svenska VetenskAkad. Handl.* 25(3/6): 24 (1899). Type: Madagascar, without specific locality, collector or date (PC-LENORMAND-lectotype (Galloway & James, 1986: 430)).
- Sticta boryana* Delise in *Mém. Soc. linn. Normandie* 2: 102 pl.8, fig. 37 (1825). *Pseudocyphellaria boryana* (Delise) D.J. Galloway in *Lichenologist* 17: 303 (1985). Type: Ile de Bourbon [Réunion], Plaine de Chicots, sur le bois mort des forêts montagneuses, *Bory de St-Vincent* s.n. (PC-THURET-holotype).
- Sticta rigidula* Delise in *Mém. Soc. linn. Normandie* 2: 97 pl. 8, fig. 34 (1825). *Stictina argyracea* f. *rigidula* (Delise) Nyl. in Hue, *Nouv. Archs Mus. Hist. nat. Paris* III, 2: 295 (1890). *Sticta argyracea* f. *rigidula* (Delise) Zahlbr., *Cat. lich. univ.* 3: 371 (1925). *Cyanisticta rigidula* (Delise) C.W. Dodge in *Beih. nov. Hedwigia* 12: 178 (1964). Type: Ile de Bourbon [Réunion], sur l'écorce, *Bory de St-Vincent* s.n. (PC-THURET-lectotype (Galloway & James, 1986: 432)).
- Sticta flavescens* Delise in *Mém. Soc. linn. Normandie* 2: 117 pl. 11, fig. 47 (1825). *Stictina argyracea* var. *flavescens* (Delise) Nyl. in Hue, *Nouv. Archs Mus. Hist. nat. Paris* III, 2: 295 (1890). *Sticta argyracea* var. *flavescens* (Delise) Zahlbr., *Cat. lich. univ.* 3: 372 (1925). *Cyanisticta flavescens* (Delise) C.W. Dodge in *Beih. nov. Hedwigia* 12: 173 (1964). Type: Ile de Bourbon [Réunion], sur l'écorce, *Bory de St-Vincent* (PC-THURET-holotype).
- Sticta aspera* Laurer in *Linnaea* 2: 41 (1827). *Sticta argyracea* var. *aspera* (Laurer) Kremp. in *Verh. zool.-bot. Ges. Wien* 18: 316 (1868). *Stictina argyracea* var. *aspera* (Laurer) Müll. Arg. in *Revue mycol.* 9: 138 (1887). *Cyanisticta aspera* (Laurer) C.W. Dodge in *Beih. nov. Hedwigia* 12: 170 (1964). Type: Mauritius, *Sieber* 40 (L 910,215-1683-lectotype (Galloway & James, 1986: 430)).

Stictina argyracea f. *insidiata* Nyl. in *Cromb., J. Linn. Soc. (Bot.)* 15: 435 (1876). *Sticta argyracea* f. *insidiata* (Nyl.) Zahlbr., *Cat. lich. univ.* 3: 371 (1925). Type: Ins. Rodriguez, I.B. Balfour 2279 (H-NYL 34058-holotype; BM-isotype). (The holotype material in Nylander's herbarium is a small scrap taken from a larger collection in Crombie's herbarium (BM) which is preserved as two separate specimens, only one of which is numbered 2279. All three specimens are labelled 'f. *insidiata* Nyl.' and not *insidiata* as appears in the protologue.)

Cyanisticta javanica Gyeln. in *Reprum Spec. nov. Regni veg.* 29: 297 (1931). Type: Java, Prov. Preanger, in monte ignivomo Papandayan, 1750 m, Schiffner 3309 (L 956.124 594-isotype).

Pseudocyphellaria horridula H. Magn. in H. Magn. & Zahlbr., *Ark. Bot.* 31A: 82 (1943). *Cyanisticta horridula* (H. Magn.) Szatala in *Annls hist.-nat. Mus. natn. hung.* 7: 41 (1956), comb. inval. Type: Hawaii ad truncos muscosos in paludosis ad Waimea, 4000', J.F. Rock 6 (W-isotype).

Pseudocyphellaria horridula var. *excrescens* H. Magn. in H. Magn. & Zahlbr., *Ark. Bot.* 31A: 83 (1943). Type: Hawaii. Maui, Iao Valley, Faurie 566 (W-not seen).

Pseudocyphellaria argyracea is a characteristic, laminally pseudocyphellate, pseudoisidiate, white-medulla species which is widespread in the palaeotropics from the Indian Ocean islands to the Pacific basin as far east as the Galapagos Islands (Weber, 1986) and as far south as New Zealand (Galloway, 1988) and southern Chile (Galloway, 1992). Typification of this species is discussed by Galloway & James (1986) and a detailed account of the morphology and anatomy is given in Galloway (1988: 64–68).

CHEMISTRY. Methyl gyrophorate, gyrophoric acid, 7 β -acetoxyhopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *Pseudocyphellaria argyracea* is slatey grey-blue to blue-black, often tinged red-brown when wet, pale grey to grey-brown when dry; it has a white medulla, a cyanobacterial photobiont and white pseudocyphellae on both upper and lower surfaces. It is characterized by numerous, evenly spaced, laminal, white pseudocyphellae which at maturity become pseudoisidiate with corticate, fingerlike pseudoisidia, concolorous with the thallus, developed in clusters, some of which may become abraded and appear granular-sorediate. New isidia often develop from older abraded structures. Superficially *P. argyracea* resembles some broad-lobed forms of *P. intricata* but differs in the pseudoisidiate clusters associated with the laminal pseudocyphellae. The taxon *P. boryana* (Galloway, 1985b; Galloway & James, 1986: 432–3) has narrower, more dissected, \pm dichotomously branching lobes and distinctive, marginal proliferations, the laminal pseudocyphellae of which are not sorediate or associated with isidia. However, it seems only to be an extreme form of *P. argyracea* and is therefore placed in synonymy with this species.

DISTRIBUTION AND ECOLOGY. *Pseudocyphellaria argyracea* is a widespread palaeotropical taxon (Fig. 1), extending from East Africa (Swinscow & Krog, 1988) to southern South America (Galloway, 1992) northwards to India (Awasthi, 1965, 1988), China (Wei, 1991) and Japan (Yoshimura, 1974), and southwards to New Zealand (Galloway, 1988). On bark of saplings and small trees and on mossy trees, rotting logs in humid, shady montane and cloud forest, often in crowns of trees, from 700 to 3650 m. Also at lower elevations in coastal sites.

SPECIMENS EXAMINED. **Africa. Tanzania:** Tanga. Usambara Mountains, Amani, Santesson 23370 (UPS); *ibid*, Brunnthaler (W, WU); Nazumbei, Brunnthaler (WU); Ukaguru Mts, road from Mandege Forest Station to Rubeho, Pocs, Harris

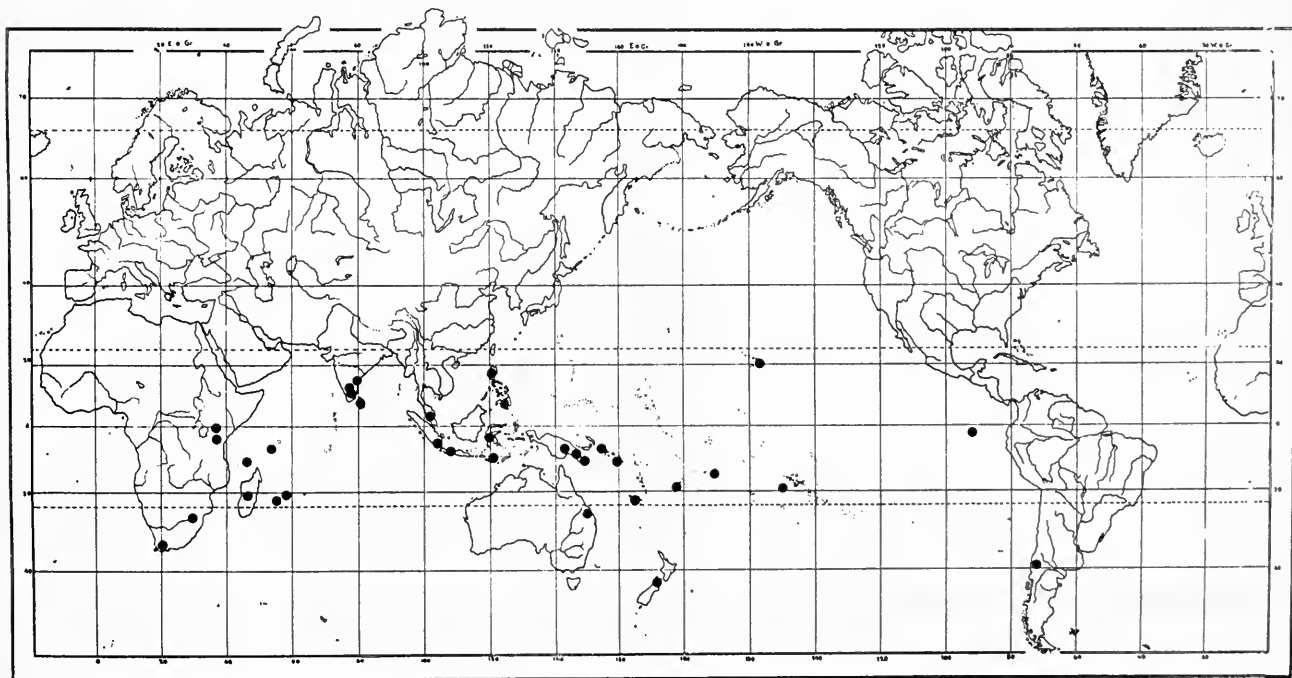


Fig. 1 Distribution of *Pseudocyphellaria argyracea* in the palaeotropics.

& *Mwanjabe* 6588 (BM); Uluguru Mts, Mwere Valley, *Pocs, Farkas, Geissler, Iversen, Steiner & Temu* 86158 (BM). **Uganda:** Masaka, Nanuzinna swamp, *Lye* L 640 (BM); Kigezi, Kinkizi, *Swinscow* 3U 56/5 (BM). **Kenya:** Mt Kenya, 200–2100 m. *Swinscow* K48.34A, K 51/3 (BM). **South Africa:** **Transvaal.** Drakensberge, *Werdermann & Oberdieck* 1849 (B). **Comoro I:** Anjouan, M'Tingui Peak, *Benson* 183 (BM). **Madagascar:** ?Andrangoloaka, ?Likora (W); sine loco, *Herb. Persoon* (L); *Roxburgh* (BM); sine loco, *Lam en Meeuse* 5966 (L). **Mauritius:** sine loco, *Robillard* (W); [ISO-TYPE] *Sieber* 40 (W); *McGregor* 1819 (BM); *Vacquois, Ayres* (BM). **Réunion:** sine loco, *Richard* (H-NYL 34064); *Cirque de Salazie, K. & A. Kalb* 26560, 26561, 26564 (Herb. Kalb); *Cirque de Cilaos, de Sloover* 17.463 (LG). **Seychelles:** Silhouette, *Gardiner* 1905 (BM). **Rodriguez Is:** *Balfour* 2279 (BM). **Sri Lanka:** Nuwara Eliya, *Meltzer* s.n. (Herb. Aptroot); *Rampodde, Almquist* (H-NYL 34065); *v. Beusekom* 290 (Herb. Aptroot); *Habgalla, Thwaites* (BM); above Pattipola, Horton Plains, *van Steenis* 19924c (L). **Thailand:** Nakhon Sawan, *Touw* 8237 (Herb. Aptroot). **Malaysia:** **Pahang.** Fraser's Hill, *Dransfield* 481 (BM); Fraser's Hill, *Burkill* 2084 (L); Fraser's Hill, *Galloway* (BM, KEP, KUL). **Indonesia.** **Sumatra:** sine loco, *Korthals* (L). **Java:** Tjibodas, *Koernich* 2a (Herb. Aptroot); *Arvidsson & Nilsson* (GB); Mt Kawi, Mt Panderman, *Groenhart* 1931, 1936, 2632 (L); Mt Gede, *Schiffner* 3289b (L); sine loco, *Junghuhn* (L); Mt Ardjuno, *Groenhart* 29, 668, 1531, 1988, 7332 (L); Mt Lawu, *Clason* 986 (L); Mt Wilis, *Groenhart* 1537, 1838 (L); Mt Pangerango, *Schiffner* (WU). **Flores:** sine loco, *Verheijen* 5201 (Herb. Aptroot). **Sulawesi:** sine loco, *De Vriese* (L). **Philippines:** **Luzon.** Pampanga. Mt Pinatubo, *Elmer* 22270 (B, BM). **Mindanao.** Butuan, *Weber* 1352 (US); Rizal, 1911, *Ramos* 13634 (BM); sine loco, *Cumming* 2156 (BM). **Papua New Guinea:** **Eastern Highlands.** Chimbu. Mt Wilhelm, *Weber & McVean* (Herb. Aptroot L54979, COLO); *Aptroot* 18235, 18333, 18651, 32786 (Herb. Aptroot); *Kashi-*

wadani 10882, 10924, 11188, 11199, 11410, 11418 (TNS); *Wade* (COLO); *McVean* 66182 (CBG); track to Mt Wilhelm, *Sipman* 21923 (B); Pindaunde Valley, *Sipman* 15905, 15906, 22098 (B); Goroka. Mt Gahavisuki Provincial Park, *Aptroot* 32420 (Herb. Aptroot); *Streimann* 18215 (CBG); Daulo Pass, *Streimann* 18110 (CBG). **Morobe.** Lake Wamba, *Koponen* 33406 (Herb. Aptroot); Mt Kaindi, *Weber & McVean* (COLO); *Streimann & Bellamy* 17665 (CBG); Herzog Mountains, *Streimann & Umba* 11015 (CBG); Gumi Divide, *Streimann* 22761 (CBG); Ekuti Divide, *Streimann* 20147 (CBG). **Southern Highlands.** Margarima, *Streimann* 24393 (CBG); Munie Logging Area, *Streimann* 23674 (CBG); Onim Forestry Station, *Streimann* 24649 (CBG); Iaro River, *Streimann* 23979 (CBG). **Milne Bay.** Woodlark Island, *Kumei* 57, 71 (CBG). **Central.** Mt Albert-Edward, *Kashiwadani* 12002 (TNS). **Western Highlands.** Tumbang Village, *Streimann* 21351, 21371 (CBG). **Solomon Islands:** **Guadalcanal Island.** Mt Popomansiu, *Hill* 9314, 9523, 9563, 9690, 9704, 9853 (BM). **Bougainville.** Lake Luralu, *Kajewsky* 1930 (BM). **New Caledonia:** Rivière Bleue, *Hill* 11689 (BM); Rivière Blanche, *Hill* 11699 (BM). **Fiji:** **Viti Levu.** Nandarivatu, *Green* (BM). **Tahiti:** sine loco, *Viellard & Panchon* (H-NYL 34064); Aorai, *v. Balgooy* (Herb. Aptroot). **Hawaiian Islands:** **Hawaii.** Waimea, *Rock* [Lichenes Sandwicensis No.6] (W). **Kauai.** Kaholnamano, *Rock* [Lichenes Sandwicensis No.11] (W). **Oahu.** Central Waianae Mts, Waianae Kai Forest Reserve, Honua Stream, *Smith* 1611 (Herb. Smith); Honouliuli Forest Reserve, Puu Kaua, *Smith* 4126 (Herb. Smith); trail to Puu Kalena, *Smith* 1549a (Herb. Smith); Koolau Mts, Koolauloa District, Kahana Valley, *Vitt* 14691 (H). **Galapagos Islands:** *Isla Pinzou.* *Sipman* L106 (COLO).

2. *Pseudocyphellaria aurata* (Ach.) Vain. in *Acta Soc. Fauna Flora fenn.* 7: 183 (1890). *Sticta aurata* Ach., *Methodus*: 277 (1803). Type: ? England, Devon, without specific locality, ex Herb. Hudson-label incomplete (H-ACH)

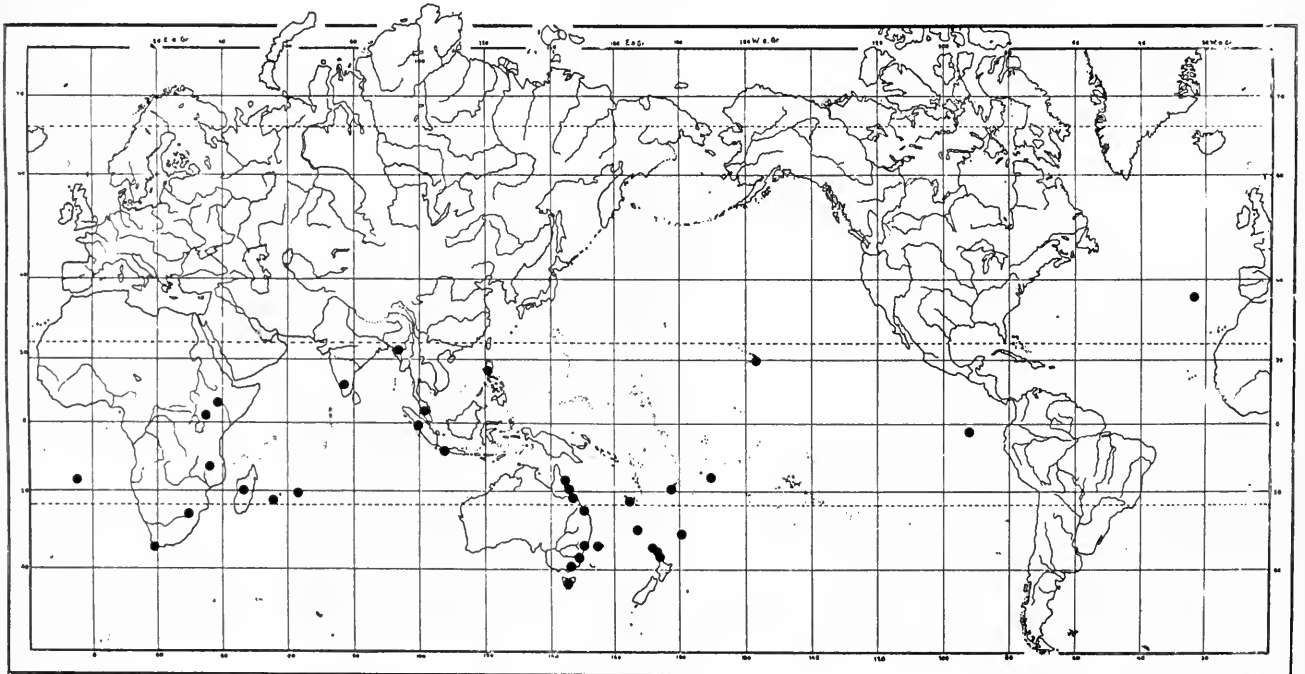


Fig. 2 Distribution of *Pseudocyphellaria aurata* in the palaeotropics.

1534-holotype). For additional synonymy see Galloway (1988).

Pseudocyphellaria aurata is bright lettuce-green tinged yellow-gold when wet, pale green-grey, often tinged or becoming reddish on storage when dry; it is a characteristic, yellow-medulla species which is widespread in tropical regions of the world, for example in Ecuador (Galloway & Arvidsson, 1990: 116–118) and is also found in drier, warmer, coastal areas in cool temperate regions, particularly in the Southern Hemisphere where it is known from New Zealand (Galloway, 1985a, 1988), eastern Australia and Chile (Galloway, 1992). Palaeotropical material closely approximates in both anatomy and morphology the description given in Galloway (1988: 68–69).

CHEMISTRY. Pulvinic acid, pulvinic dilactone, calycin, 3 β -acetoxyfern-9(11)-en-12-one, 3 β -acetoxyfern-9(11)-en-12 β -ol, fern-9(11)-ene-3 β , 12 β -diol, 3 β -acetoxyfern-9(11)-en-19 β -ol, 3 β -hydroxyfern-9(11)-en-12-one, lupeol acetate (Wilkins & Elix, 1990).

OBSERVATIONS. *Pseudocyphellaria aurata* is a cosmopolitan species having a yellow medulla, a green photobiont, yellow pseudocyphellae on the lower surface, and prominent, marginal, labriform, \pm linear yellow soralia, that often erode back the lower surface and contain coarse, granular yellow soredia. Apothecia rather rare, submarginal, distinctly pedicellate, exciple concolorous with thallus, margins ragged, yellow-sorediate. Spores brown, broadly fusiform-ellipsoid, 3-septate (25-)30–32 \times 6–7 μ m.

DISTRIBUTION AND ECOLOGY. *Pseudocyphellaria aurata* occurs on trees, shrubs and rocks in both open, sunny sites as well as in the forest canopy and on branches and twigs in moderate shade in montane forests. From sea level to 2300 m. Widespread in the tropics (Fig. 2) and in cool temperate regions (Galloway, 1988, 1992; Galloway & Arvidsson, 1990).

SPECIMENS EXAMINED. **Africa. Tanzania:** Arusha National Park. Mt Meru, *Renvoize* 2493c (BM). **Kenya:** Mt Marsabit, *Lye* (BM). **Uganda:** Lake Mulehe, *Swinscow* (BM). **Malawi:** Zomba Plateau, *Jellicoe* (BM). **South Africa: Cape Peninsula.** Hout Bay, *Maas Geesteranus* 14659 (Herb. Aptroot); near Knysna, *Werdermann & Oberdieck* 913b (B); Cape of Good Hope, *Ecklon* (B); Table Mt, *Eaton* (BM). **Natal. Sim** (BM). **Transvaal.** Kowyns Pass near Graskop, *Sipman* 19.926 (B); Long Tom Pass, *Sipman* 20.094 (B); Drakensberge, *Werdermann & Oberdieck* 1855 (B). **Madagascar:** Imarina, *Cowan* (BM). **Réunion:** sine coll. (BM); southern slope of Piton des Niegues, near Cilaos, *Arvidsson & Nilsson* 2536 (GB); Cirque de Cilaos, *de Sloover* 17.471, 17.473, 17.631, 17.780 (LG). **Rodriguez I: Balfour** (BM). **Malaysia: Pahang.** Fraser's Hill, *Dransfield* 517 (BM); Fraser's Hill, *Galloway* (BM, KEP, KLU); Cameron Highlands, Tanak Rata, *Degelius* As-547, As-550 (UPS). **Indonesia. Sumatra:** Bukittinggi, *Hensen* (Herb. Aptroot). **Java:** Tjibodas, *Koernich* 2b (Herb. Aptroot). **Philippines: Luzon.** Benguet. Mt Santo Tomas, *Aptroot* 20449 (Herb. Aptroot); *Sipman* 21751 (B); Baguio, Luneta Hill, *Degelius* As-905 (UPS). **New Guinea: Morobe.** Edie Creek Road, *Streimann* NGF 39103 (CBG); *v. Royen* NGF 16288 (Herb. Aptroot); Kwama River Valley, *Koponen* 33232 (Herb. Aptroot); Upper Watut River, *Streimann* 17072 (CBG); Herzog Mountains, *Streimann & Umba* 10988, 11137 (CBG); Honzeukngon village, *Aptroot* 17773 (Herb.

Aptroot); Pouyu Village, *Streimann & Tamba* 12575, 12693 (CBG); Upper Nawata Band, *Streimann* 33973 (CBG); Manki Trig, *Streimann & Bellamy* 12942 (CBG); Mt Susu, *Streimann* 34182 (CBG); Kauli Lake, *Streimann* 34099 (CBG); Mt Kaindi, *Streimann* 33418 (CBG). **Madang.** Finisterre Range. Teptep Village, *Aptroot* 32286 (Herb. Aptroot). **Eastern Highlands.** Lapegu, *Streimann* 18275, 18396, 18427, 18443 (CBG); Mt Michael, *Streimann* 18786 (CBG); Goroka. Mt Gahavisuki Nature Reserve, *Aptroot* 18848 (Herb. Aptroot). **Western Highlands.** Kagamuga, *Streimann* 21701 (CBG). **New Caledonia:** sine loco, *Compton* 716 (BM). **Norfolk Island:** Mt Pitt Reserve, Duncombe Road, *Streimann* 34595 (CBG); Broken Pine, *Elix* 18315 & *Streimann* (BM). **Kermadec I.: Cheeseman** (BM). **Hawaiian Islands: Oahu.** Waianae Mts, Honouliuli Forest Reserve. Puu Kaua, *Smith* 4126 (Herb. Smith); Waianae Kai Forest Reserve, Honua Stream, *Smith* 1611 (Herb. Smith). **Fiji: Viti Levu.** Nadarivatu. Nadala, *Degener* 31807b (B); District Commissioner House, *Degener* 31814ad (B); Mba, *Smith* 5965 (BM). **Samoa:** sine loco, *Powell* (BM). **Galapagos Islands: Isla Charles.** Trail from Black Beach to highlands, *Weber & Lanier* (COLO); *Weber* 328, 427 (COLO). **Isla Duncan.** Summit, *Cavagnaro* (COLO). **Isla Isabella.** Volcan Cerro Azul, *Sipman* L-67 (COLO); *Weber & Lanier* (COLO). **Isla San Cristobal.** West of El Junco, *Lanier* (COLO).

3. *Pseudocyphellaria beccarii* (Kremp.) D.J. Galloway, comb. nov.

Fig. 3.

Basionym: *Sticta beccarii* Kremp. in *Nuovo G. bot. ital.* 7: 11 (1875). *Stictina beccarii* (Kremp.) Müll. Arg. in *Flora, Jena* 65: 301 (1882). Type: Sarawak, *O. Beccari*, Lichenes Bornenses, No. 121, 1866 (M-lectotype, selected here; BM, M-isolectotypes).

Stictina fragillima var. *subpunctulata* Nyl. in *Leight.*, *Trans. Linn. Soc. Lond.* 27: 164 (1869). *Stictina subpunctulata* (Nyl.) Stizenb. in *Flora, Jena* 81: 138 (1895). *Sticta subpunctulata* (Nyl.) Hue in *Nouv. Arch. Mus. Hist. nat. Paris* IV, 3: 54 (1901). *Pseudocyphellaria subpunctulata* (Nyl.) Vain. in *Philipp. J. Sci. sect. C, Bot.* 8: 119 (1913). *Cyanisticta subpunctulata* (Nyl.) Szatala in *Annls hist.-nat. Mus. natn. hung.* 7: 41 (1956), comb. inval. Type: Ceylon, Central Province, *G.H.K. Thwaites* C.L. 22 (BM-lectotype, selected here).

Stictina junghuhniana Müll. Arg. in *Flora, Jena* 65: 300 (1882). *Pseudocyphellaria junghuhniana* (Müll. Arg.) D.D. Awasthi in *Beih. nov. Hedwigia* 17: 104 (1965). Type: In Insula Java, *Junghuhn* (L-910,215–1406-lectotype, selected here).

Stictina junghuhniana var. *laevis* Müll. Arg. in *Flora, Jena* 65: 300 (1882). *Stictina subpunctulata* var. *laevis* (Müll. Arg.) Stizenb. in *Flora, Jena* 81: 128 (1895). *Sticta subpunctulata* var. *laevis* (Müll. Arg.) Zahlbr., *Cat. lich. univ.* 3: 399 (1925). *Pseudocyphellaria junghuhniana* var. *laevis* (Müll. Arg.) D.D. Awasthi in *Beih. nov. Hedwigia* 17: 104 (1965). Type: Ceyloniae, in montanis cum forma genuina speciei, altit. circ. 6000-pedali, *Nieter* (G-not seen).

Thallus irregularly spreading in entangled clones, 8–15(–25) cm diam., loosely attached centrally, apices free, ascending. **Lobes** linear-elongate, 3–8(–15) mm wide, 1–5(–10) cm long, \pm dichotomously to irregularly branching, contiguous or discrete at margins, \pm imbricate centrally, apices divergent,

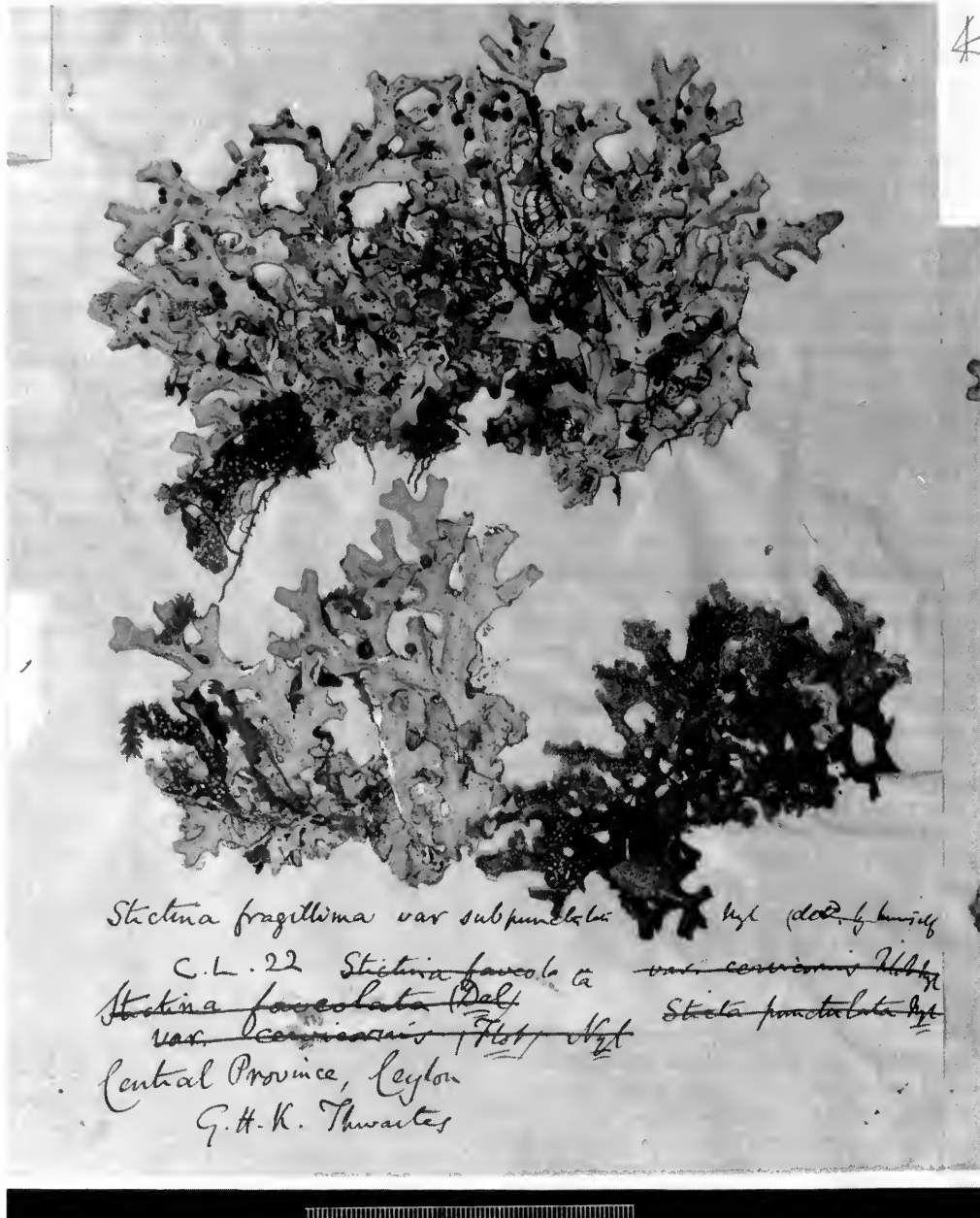


Fig. 3 *Pseudocyphellaria beccarii*. Lectotype *Stictina fragillima* var. *subpunctulata* (BM). Scale in mm.

rounded, truncate or sharply to bluntly furcate. Margins entire, noticeably thickened, ridged below and often conspicuously pseudocyphellate, very rarely with occasional small lobules developed. Upper surface dark grey-black or blue-black, suffused red-brown at apices, pale glaucous buff or greyish when dry, conspicuously deeply to shallowly punctate-depressed or dimpled, irregular to undulate or wrinkled, not faveolate, coriaceous, matt or shining in parts, maculate, without isidia, phylidia, pseudocyphellae or soredia.

Medulla white. Photobiont cyanobacterial. Lower surface pale buff or whitish at margins, red-brown to black centrally or sometimes uniformly pale brown from margins to centre, irregularly wrinkled to \pm bullate, tomentum rather variable, from scattered thin patches centrally to densely and uni-

formly developed from margins to centre, pale buff or whitish to red-brown or blackened. Pseudocyphellae white, widely scattered to common and \pm crowded, round to irregular, 0.1–1(–1.5) mm diam., conical-verrucose, margins distinctly raised and sharply defined, concolorous with lower cortex, decorticate area flat to \pm concave, projecting above thin tomentum or usually sunk in thick tomentum, often \pm conspicuous at margins.

Pycnidia mainly marginal, crowded in lines, rarely scattered on upper surface, ostiole hemispherical brown-black, 0.1 mm diam.

Apothecia marginal or submarginal, rarely laminal, sparse to moderately frequent, rounded to subirregular, 2–5 mm diam., sessile to subpedicellate, exciple coarsely verrucose-scabrid, obscuring disc when young, pale buff to brown, disc

to dark red-brown, to \pm blackened, consistently darker than margin, concave at first, plane to subconvex at maturity, matt, smooth, epruinose. *Epithecium* pale yellow-brown, 12–15 μm thick. *Hymenium* colourless, 100–115 μm tall. *Ascospores* pale brown, 3-septate, ellipsoid, apices pointed, $33.5\text{--}42.5$ (-44.5) \times (6.5–) 8.5–11 μm .

CHEMISTRY. Tenuiorin, methyl gyrophorate, gyrophoric acid, 7 β -acetoxypopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *Pseudocyphellaria beccarii* is characterized by a white medulla; a cyanobacterial photobiont; a dimpled, punctate-impressed upper surface; \pm dichotomously branching lobes with entire margins; scattered, flecklike white pseudocyphellae on the lower surface; and a two-hopane chemistry with tenuiorin, methyl gyrophorate and gyrophoric acid as accessory substances. It is distinguished from *P. insculpta* in the absence of marginal isidia and phyllidia, from *P. sulphurea* in having a cyanobacterial photobiont, and from *P. semilanata* which has scattered white pseudocyphellae on the upper surface.

DISTRIBUTION AND ECOLOGY. Widespread in the palaeotropics (Fig. 4), from Madagascar eastwards to Fiji and Samoa but not known from Hawaii. Also in north-eastern Australia. An epiphyte of montane rainforest and mossy cloudforest on trees and shrubs, 1500–2800 m.

SPECIMENS EXAMINED. **Madagascar:** sine loco, *Thompson* (M). **Sri Lanka:** sine loco, *Beccari* 12 [Crittogame di Ceylan No. 12] (M); Nuwara Eliya, ?*Blallu* 74 (W). **Burma:** sine loco, *Lobb* (BM). **Malaysi:** **Sabah.** Mt Kinabalu, *Sipman & Tan* 30960, 31084, 31377 (B); *Richards* (BM); *Clarke* 86 (BM). **Indonesia.** **Java:** Mt Ardjuno, *Groenhart* 1516, 1852, 1993, 1998, 2042, 4615, 7245, 7327, 7329 (L); Mt Kawi, *Groenhart* 1829, 1951, 1963, 7255 (L); Mt Lawu, *Clason* 982 (L); Mt Wilis, *Groenhart* 1538 (L); Batu, *Roomaker* 1985

(L); Mt Gede, *Groenhart* 7271 (L); Mt Megamendung, *Schiffner* 1159, 3351 (L, WU). **Kalimantan:** sine loco, *Beccari* (M). **Philippines.** **Luzon:** Benguet, Mt Pulog, *Jacobs* B47 (Herb. Aptroot); *Curran, Merritt & Zschokke* (US); Pauai, *McGregor* (E, US); Pampanga. Mt Pinatubo, *Elmer* 22270 (B, BM); Laguna. Mt Banajao, *Merrill* 7525 (US); Mt Malinao, *Edano* 37208 (L). **Mindoro:** Alag River, *Merrill* 5497 (US). **Papua New Guinea: Eastern Highlands.** Chimbu. Mt Wilhelm, *Sipman* 21959, 22137 (B); *Borgmann* 776, 896 (B); *Kashiwadani* 10845, 10917, 10965, 11080 (TNS); *McVean* 66149 (CBG); Lake Aunde, *Aptroot* 18466 (Herb. Aptroot); Pindaunde Valley, *Weber & McVean* (B, COLO); Goroka. Daulo Pass, *Streimann* 17989 (CBG). **Morobe.** Cromwell Mountains, Siwea, *Koponen* 30545 (Herb. Aptroot); Huon Peninsula, Mt Rawlinson, *Hoogland* 9315 (Herb. Aptroot, COLO); Mt Missim, *Bellamy* 203 (CBG); Ekuti Divide, *Streimann* 20121, 20168, 20187, 20212, 34148 (CBG); Wagau-Malolo Track, *Streimann* 19577 (CBG); Upper Watut River, *Streimann* 23137 (CBG); near Honzeukngon village, *Aptroot* 17998, 18041 (Herb. Aptroot); Rawlinson Range, *Strong Clemens* 12490 (COLO); Aiuwa-Bakia Track, *Streimann & Tamba* 12281 (CBG); Yinimba, *Streimann* 19710 (CBG); Mannasat, *Hoogland* 9466 (COLO). **Central.** Mt Albert-Edward, *Kashiwadani* 11748, 11770, 11816, 11982 (TNS). **Western Highlands.** Nebilyer River, *Streimann* 20599 (CBG); Mur Mur Pass, *Streimann* 21196, 22404 (CBG). **Southern Highlands.** Munie Logging Area, *Streimann* 23248, 23309, 23613, 23615 (CBG); Onim Forestry Station, *Streimann* 24639 (CBG); Enga. Mt Hagen-Wabag Road, *Streimann* 21256 (CBG). **Solomon Islands: Guadalcanal Island.** Mt Popomansiu, *Hill* 9290, 9560, 9572, 9632, 9694, 9706 (BM); Mt Gallego, *Hill* 8172 (BM). **Kolombangara Island.** Ridge west of Kolombangara River, *Hill* 10686 (BM). **Society Islands: Raiatea.** Tetoorea, 200 m, *Moore* L26 (Herb. Aptroot). **Fiji: Viti Levu.** Mt Tomanivi [Victoria], *Smith* 5205a (BM); Mt Victoria, *Selling* (S); *Lam* 6831 (L);

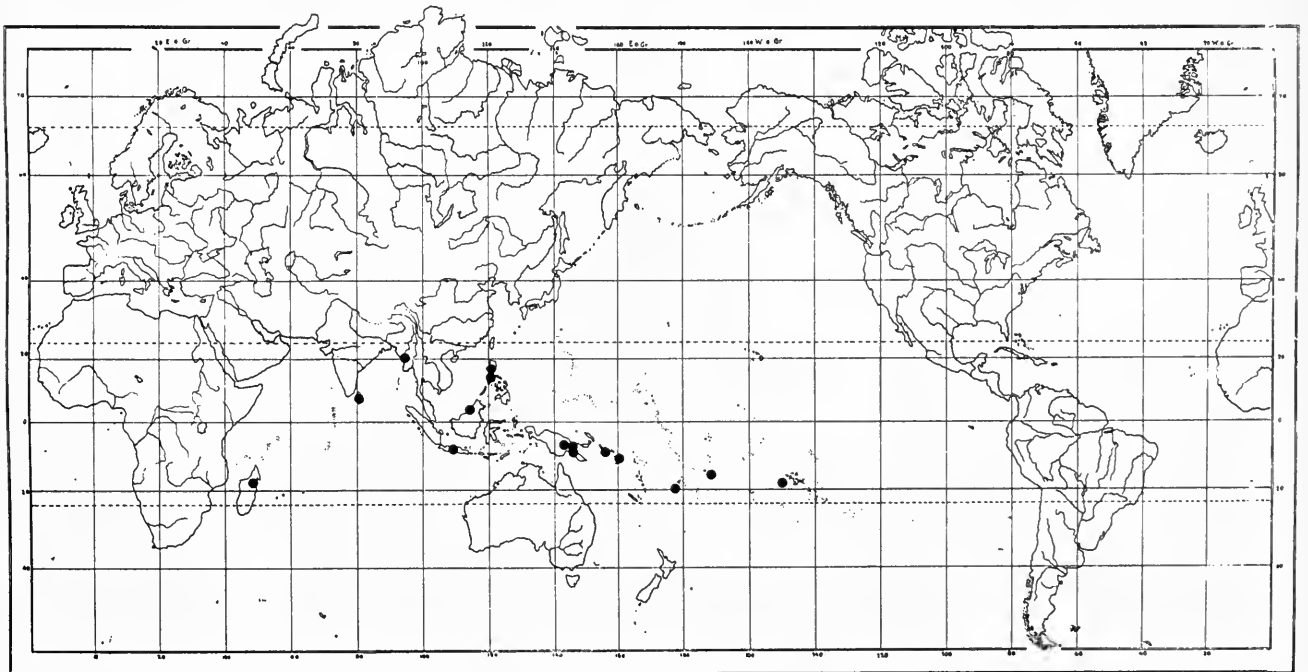


Fig. 4 Distribution of *Pseudocyphellaria beccarii* in the palaeotropics.

Mt Tomanivi [Victoria], *Smith* 5205a (US); Ra, ridge from Mt Namama toward Mt Tomanivi, *Smith* 5712 (BM). **Samoa:** **Upolu.** Mountains near Tiave, *Schultz-Motel* 4350 (B).

4. ***Pseudocyphellaria carpoloma*** (Delise) Vain. in *Hedwigia* 37: 34 (1898). *Sticta carpoloma* Delise in *Mém. Soc. linn. Normandie* 2: 159 pl. 19, right hand figure (1825). *Stictina carpoloma* (Delise) Nyl., *Syn. meth. lich.* 1(2): 339 (1860). *Saccardoia carpoloma* (Delise) Trevis., *Lichenotheca veneta* exs. no. 75 (1869). *Cyanisticta carpoloma* (Delise) Gyeln. in *Reprium Spec. nov. Regni veg.* 29: 2 (1931). Type: New Zealand, 'Sur les vieux arbres à la Nouvelle Zélande', Bay of Islands, 1824, ?R.P. Lesson (PC-LÉNORMAND-holotype). For additional synonymy see Galloway (1988: 80–85).

Pseudocyphellaria carpoloma is bright lettuce-green to olive-green when wet, pale olivaceous-greenish when dry; it is a characteristic dichotomously branching, white-medulla, green-photobiont species with yellow pseudocyphellae below, which is widespread in New Zealand (Galloway, 1988) but has not been previously correctly identified from tropical regions. It is discussed in detail in Galloway (1988: 80–85). Earlier tropical records of *P. carpoloma* such as Magnusson (1940, 1956), Magnusson & Zahlbruckner (1943), Szatala (1956) refer to specimens of *P. gilva*, a cyanobacterial species.

CHEMISTRY. Methyl evernate, tenuiorin, methyl gyrophorate, evernic acid (tr.), gyrophoric acid (tr.), hopane-7 β , 22-diol, hopane-6 α , 7 β , 22-triol, 7 β -acetoxyhopane-6 α , 22-diol (tr.), 6 β -acetoxyhopane-7 β , 22-triol (tr.), norstictic (tr.), stictic, cryptostictic, and constictic acids, pulvinic dilactone, pulvinic acid and calycin.

OBSERVATIONS. *Pseudocyphellaria carpoloma* is characterized by dichotomously branching lobes with entire margins

and a distinctive, faveolate upper surface. It has a white medulla, a green photobiont and prominent yellow pseudocyphellae on the lower surface and projecting from the margins. Spores grey-brown, oval-ellipsoid, thickened 1-septate to 3-septate at maturity, (20–)22–25(–27) \times 7–11 μ m.

DISTRIBUTION AND ECOLOGY. In the palaeotropics known so far only from Papua New Guinea and Norfolk Island from humid forest at 900 and 2500 m (Fig. 5). It is probably more widespread in the palaeotropics and is need of further collection.

SPECIMENS EXAMINED. **Papua New Guinea:** Madang. Finisterre Range. Teptep Village, *Aptroot* 31927 (Herb. Aptroot). **Norfolk Island:** Mt Bates, *Henderson* (E).

5. ***Pseudocyphellaria clathrata*** (De Not.) Malme in *Ark. Bot.* 26A(14): 9 (1934). *Sticta clathrata* De Not., *Osserv. Sticta:* 19 (1851). *Crocodia clathrata* (De Not.) Trevis., *Lichenotheca veneta* exs. no. 75 (1869). Type: Brazil, in sylvis insulae S. Sebastiano, 1839, *Casaretto* (BM-lectotype (Galloway & Arvidsson, 1990: 119)). For additional synonymy see Galloway & Arvidsson (1990: 119).

Pseudocyphellaria clathrata is bright lettuce-green with a yellow-gold tinge when wet, grey-green often suffused reddish when dry or on storage; it is a characteristic rosette-forming to irregularly spreading, yellow-medulla species which is widespread in tropical regions (Galloway & Arvidsson, 1990; Galloway, 1993). Palaeotropical material examined agrees in all respects with the anatomical and morphological details given in Galloway & Arvidsson (1990: 121–126).

CHEMISTRY. Similar to that of *P. arvidsonii* and *P. aurata* (Galloway & Arvidsson, 1990) containing calycin, pulvinic

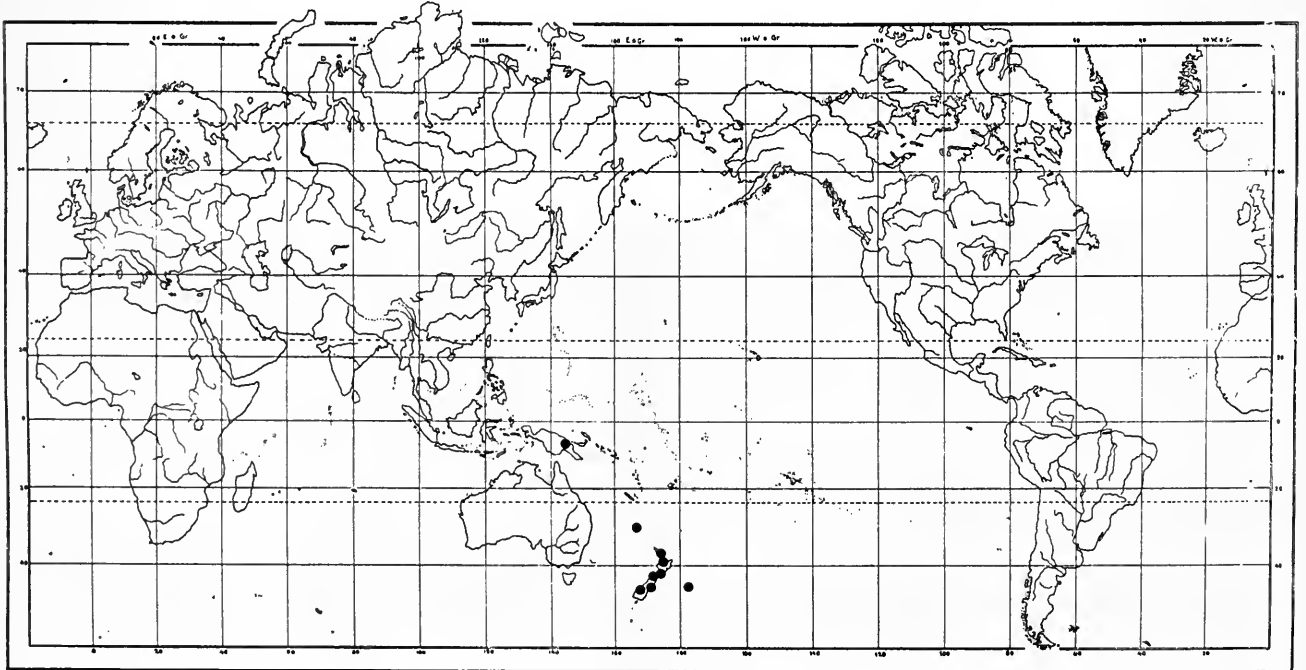


Fig. 5 Distribution of *Pseudocyphellaria carpoloma* in the palaeotropics.

lactone, pulvinic acid and a mixture of unidentified fernene triterpenoids.

OBSERVATIONS. *Pseudocyphellaria clathrata* is a widely distributed pantropical species having rather large, broadly rounded to subdichotomously or irregularly branching lobes with entire, non-sorediate, non-phyllidiate margins and is characterized by a yellow medulla, a green photobiont, yellow pseudocyphellae on the lower surface, a glabrous to partly pubescent or tomentose upper surface which is \pm distinctly punctate-impressed, and distinctly pedicellate marginal to submarginal apothecia. Apothecia distinctly pedicellate, areolate-scabrid to white-tomentose, concolorous with thallus. Spores fusiform-ellipsoid, pointed at one or both ends, 3-septate at maturity, pale red-brown, $(15.5\text{--})18\text{--}20.5\text{--}(22.5) \times 3.5\text{--}4.5 \mu\text{m}$.

DISTRIBUTION AND ECOLOGY. Widespread in tropical regions of the world (Swinscow & Krog, 1988; Galloway & Arvidsson, 1990; Galloway, 1993) and recently collected in northern India by Dr K.P. Singh (Fig. 6). In humid montane forest, in canopy branches and main branches of shrubs and trees, rarely on rocks, 400–1600 m.

SPECIMENS EXAMINED. **Africa.** **Uganda:** Kabale, *Burnet* 230 (BM); West Mengo, *Lye* L 196 (BM). **Zimbabwe:** sine loco, *Sim* (BM). **Tanzania:** Ngorongoro Crater, *Pocs & Chuwa* 89027/Z (BM); Usumbara Mountains, Amani, *Moberg* 1491b (UPS). **Kenya:** Ngong Hills, *Meyink* (BM); Mt Kenya, *Swinscow* (BM); Kakamega District, *Santesson* 21764 (UPS); Kajiado District, Ngong Hills, *Moberg* 1413 (UPS). **South Africa:** **Cape Province.** Table Mountain, *Sipman* 20.186 (B); Disa Gorge, Table Mt, *Pillans* (BM). **Angola:** Golungo Alto, *Welwitsch* (BM). **Madagascar:** sine loco, *Sykora*, 1894 (WU); Imerina, Andrangoloaka, 1880, *Hidebrandt* 2156 (WU); Imerina, *Wills* (BM). **Réunion:** sine loco, *Lepervanche Mezières* (M); southern slopes of Piton des Nieves, near

Cilaos, *Arvidsson & Nilsson* 2538 (GB); Cirque de Cilaos, *de Sloover* 17/472 (LG). **Java:** Mt Ardjuno, *Groenhart* 9769 (L). **Tjibodas,** *Arvidsson & Nilsson* 2494 (GB). **Philippines:** **Luzon.** Benguet, Bangio, *Elmer* 8991 (BM). **Papua New Guinea:** **Eastern Highlands.** Goroka, Lapegu, *Streimann* 18272, 18289 (CBG). **Morobe.** Mt Kaindi, *Kashiwadani* 10516 (TNS); Kauli Lake, *Streimann* 34079, 34092 (CBG); Yinimba, *Streimann* 19177 (CBG). **Western Highlands.** Baiyer River Sanctuary, *Streimann* 21105 (CBG); Kagamunga, *Streimann* 21301 (CBG); Minj, *Streimann* 21504 (CBG). **New Caledonia:** Ile des Pins. Tribu de Gadji, *Hill* 12099 (BM). **Norfolk Island:** sine loco, *F. Bauer* (W).

6. *Pseudocyphellaria crocata* (L.) Vain. in *Hedwigia* 37: 34 (1898). *Lichen crocatus* L., *Mant. pl.*: 310 (1771). Type: India, without specific location, *König* (LINN 1273.137-holotype). For additional synonymy see Galloway (1988: 113) and Galloway & Arvidsson (1990: 126).

Sticta xanthosticta Pers. in *Gaudich., Voy. Uranie*: 201 (1827). Type: [Hawaii] in insulis Sandwicensibus, *Gaudichaud* (L 910.187.685-lectotype, selected here).

Sticta crocata f. *sandwicensis* Zahlbr. in *Rech., Denkschr. Akad. Wiss. Wien* 88: 29 (1911). *Cyanisticta sandwicensis* (Zahlbr.) Gyeln. in *Reprim Spec. nov. Regni veg.* 29: 6 (1931). Type: Hawaii. Vulkan Kilauea, auf arten von *Metrosideros*, April 1905, *N. Rechinger* 2544 (W-lectotype, selected here).

Pseudocyphellaria hawaiiensis H. Magn. in *Acta Horti gothoburg.* 14: 21 (1940). *Cyanisticta hawaiiensis* (H. Magn.) Räsänen in *Suomal. elain-ja kasvit. Seur. van. kasvit. Julk.* 20(3): 17 (1944). Type: Hawaii. Molokai, between Upper Mountain Camp and Pepeopae, 9 July 1938, *O. Selling* 5842 (UPS-isotype).

Cyanisticta hawaiiensis var. *scrobiculata* Räsänen in *Suomal. elain-ja kasvit. Seur. van. kasvit. Julk.* 20(3): 17 (1944).

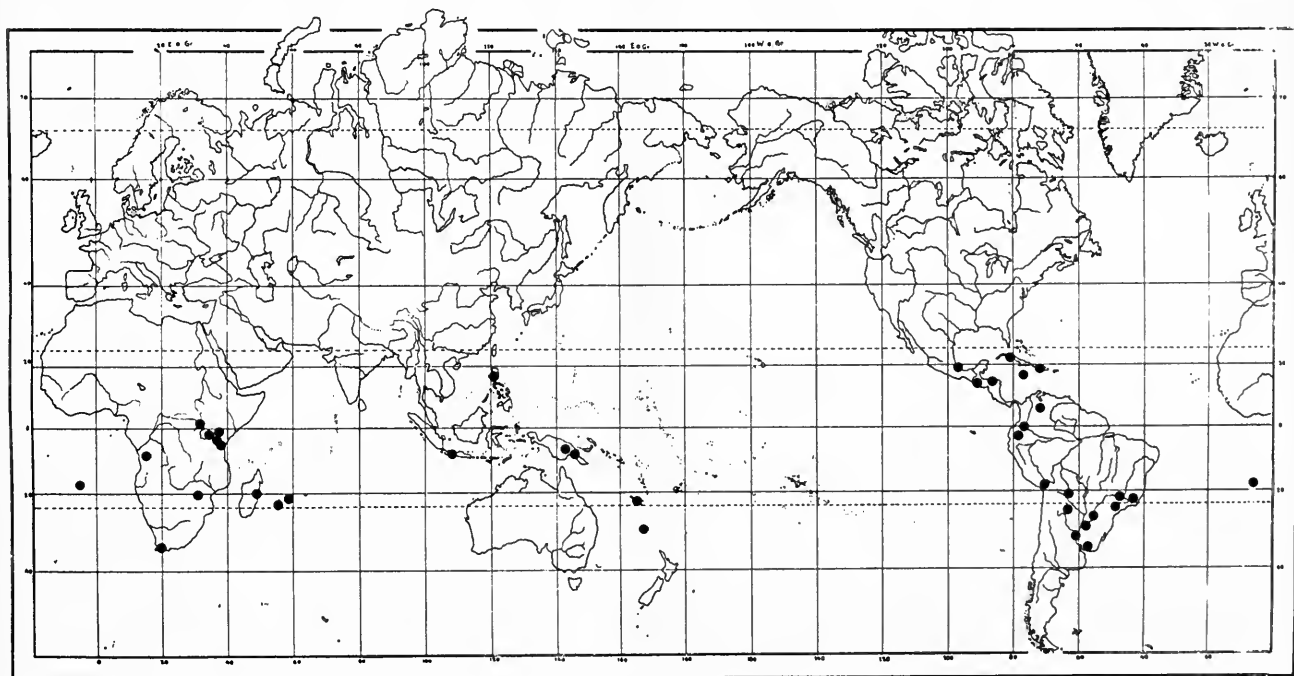


Fig. 6 Distribution of *Pseudocyphellaria clathrata* in the palaeotropics.

Type: Tahiti. Sine loco, *Vieillard* (H-not seen).

Cyanisticta hawaiiensis var. *xanthocardia* Räsänen in *Suomal. elain-ja kasvit. Seur. van. kasvit. Julk.* 20(3): 17 (1944).

Type: Tahiti. Sine loco, *Vieillard* (H-not seen).

Pseudocyphellaria crocata is dark slate-blue to blue-black or glaucous brownish often suffused red-brown when wet, pale olivaceous grey or blue grey to red-brown when dry; it is widespread in both tropical and temperate regions of the world and shows both throughout and within its range a considerable plasticity of form which has led to an extensive synonymy. Palaeotropical material is also very variable but within the range of anatomy and morphology recorded by Galloway (1988: 115–118). Hawaiian material recorded as *P. hawaiiensis* (Magnusson, 1940; Magnusson & Zahlbruckner, 1943) tends to have narrower, \pm dichotomously branching lobes with the soralia often restricted to small, scattered, marginal clumps, but in a range of recently collected material (Prof. C.W. Smith, pers. comm.) a complete sequence from broad-lobed, laminally and marginally sorediate forms to narrow-lobed, \pm dichotomously branching, sparsely marginally sorediate forms was observed, all of which fall within the species range of variation.

CHEMISTRY. Tenuiorin, methyl gyrophorate, gyrophoric acid (tr.), hopane-6 α , 7 β , 22-triol (major), 6 α -acetoxyhopane-7 β , 22-diol (tr.), 7 β -acetoxyhopane-6 α , 22-diol (tr.), hopane-7 β , 22-diol (tr.), \pm physciosporin (tr.) norstictic (tr.), stictic, cryptostictic, constictic and \pm salazinic acids, pulvinic acid and pulvinic dilactone (Elix et al., 1992).

OBSERVATIONS. *Pseudocyphellaria crocata* is characterized by a white medulla; a cyanobacterial photobiont; yellow laminal and marginal soralia on the faveolate to plane upper surface, and yellow pseudocyphellae on the lower surface. Apothecia are rather variable in occurrence varying from moderately common to rare or absent. Spores are broadly

ellipsoid, smoky olive-brown to dark brown, thickened 1-septate to irregularly 3-septate, straight or slightly curved, 22.5–27(–29.5) \times 7–9 μ m. It has a characteristic chemistry including hopane-6 α , 7 β , 22-triol, stictic acid metabolites, tenuiorin and methyl gyrophorate and yellow pigments. It is distinguished mainly by its soredia from other members of the *P. crocata*-group; *P. gilva* has neither soredia nor isidia or phyllidia; *P. crocatoides* has characteristic marginal lobules but no soredia or true isidia; *P. neglecta* has marginal and laminal phyllidia which may erode and become pseudosorediate; while *P. desfontainii* has terete to subsquamiform isidia which never become sorediate.

DISTRIBUTION AND ECOLOGY. Widely distributed in the palaeotropics and neotropics and in cool temperate zones of both Northern and Southern Hemispheres (Fig. 7). One of the most widely distributed species in the genus. It occurs in a wide variety of habitats from sea level to 4200 m (in Papua New Guinea) as an epiphyte of trees, shrubs, on rotting logs and on the forest floor, on both shaded and sunny rocks, and on soil in alpine grasslands. In the palaeotropics it occurs most commonly in humid, shaded woodlands, montane forest, cloudforest and alpine grasslands.

SPECIMENS EXAMINED. **Africa. Tanzania:** Kiliminjaro, *Bigger* 1966 (BM). **Kenya:** Mt Marsabit, *Lye* L660 (BM); Aberdare Mts, *Swinscow* (BM). **Uganda:** Usumbara Mts, *Holst* 2665 (BM); Sasa River above Bulambuli, *Lye* L 501 (BM). **South Africa: Cape of Good Hope.** Table Mountain, *Wedermann & Oberdieck* 48 (B); ?Tafelberg, *Wilms* (B). **Transvaal.** Houbosdorp, *Sipman* 19.786 (B); Kowyns Pass near Graskop, *Sipman* 19.936 (B); Long Tom Pass, *Sipman* 20.093 (B). **Madagascar:** sine loco, *Baron* (BM). **Réunion:** Cirque de Cilaos, auf der Strasse zwischen Cilaos und Ilet a Cordes auf den Col du Taibit, *K. & A. Kalb* 26567 (Herb. Kalb); Piton de la Grande Montée, près des sources Reihlac, *de Sloover*

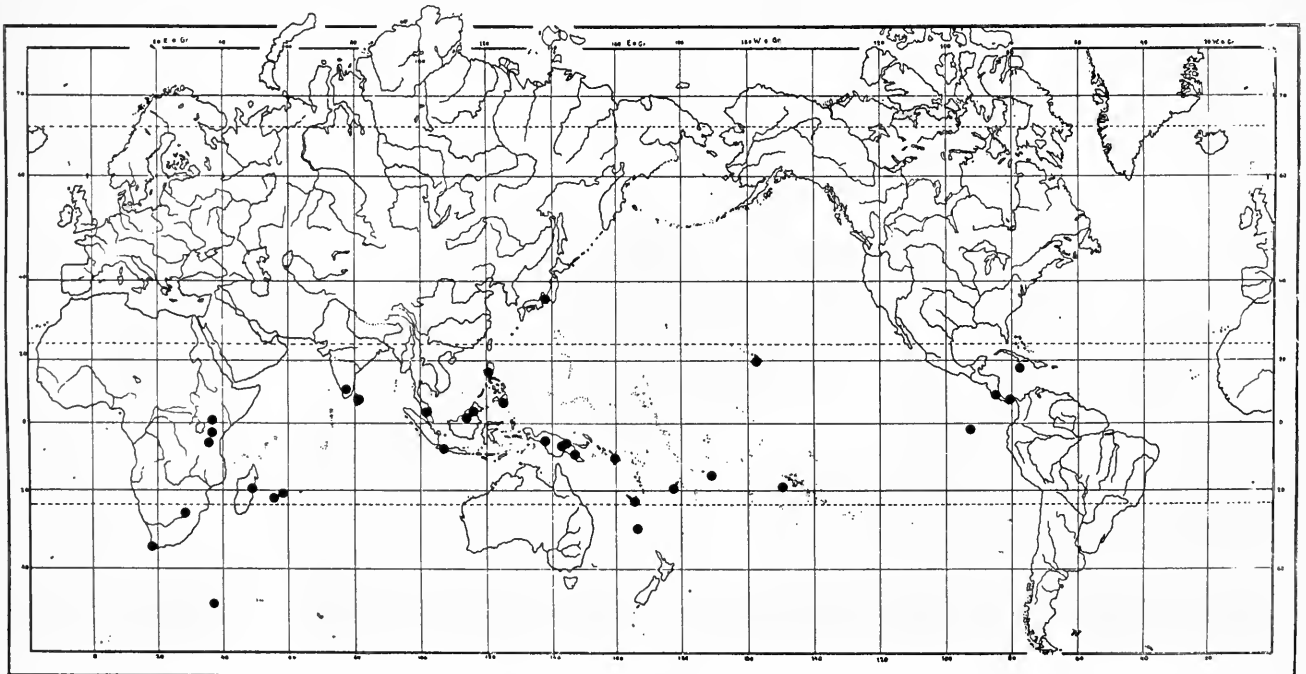


Fig. 7 Distribution of *Pseudocyphellaria crocata* in the palaeotropics.

17.257 (LG); SW du Piton Mare-a-Boue, *de Sloover* 17.299 (LG); Cirque de Cilaos, *de Sloover* 17.538, 17.577, 127.927 (LG). **Mauritius:** Pouce Mt, *Ayres* (BM); Curepipe, sine coll. (BM). **Sri Lanka:** Central Province, *Thwaites* C.L. 24 (BM). **Malaysia:** **Pahang.** Fraser's Hill, *Burkill* 2099 (L); Fraser's Hill, *Galloway* (KEP); Cameron Highlands, Tanak Tara, *Degelius* As-567 (UPS). **Sabah.** Mt Kinabalu, *Sipman & Tan* 31105, 31079, 31024 (B). **Sarawak.** Gunung Mulu National Park, *Argent & Coppins* 5116 (BM). **Indonesia.** **Sulawesi:** sine loco, Herb. Lugd. Batav. (L). **Java:** Tjibodas, *Koernich* 6a (Herb. Aptroot); *Sipman & Zainal* 30094 (B); Kawi Mountains. Mt Panderman, *Groenhart* 1934 (Herb. Aptroot); sine loco, *Jelinek* (B); Idgen Plateau, Kebun Djampit, *Pos* 7379 (B); sine loco, *Junghuhn* (L); Mt Pangerango, *Schiffner* 3288 (W); Cibodas Botanical Garden, *Arvidsson & Nilsson* 2488 (GB). **Philippines:** **Luzon.** Benguet, Mt Santo Tomas, *Aptroot* 20447, 20448, 20452, 20453 (Herb. Aptroot); Mt Pulog, *Merrill* 6458 (BM). **Mindanao.** Mt Apo, *Copeland* 1093 (BM). **West Irian:** Eipomek-Tal, *Hiepko & Schultze-Motel* 2019, 2277 (B); Carstensz Mts, *Hope* (COLO). **Papua New Guinea:** **Morobe.** Saruwaged, *Sipman* 24336, 24386, 24429, 24462 (B); Kaisinik, *Kashiwadani* 10448, 10686, 10745, 10760 (TNS); Mt Missin, *Kashiwadani* 10428 (TNS); Rawlinson Range, *Strong Clemens* 12444 (COLO); Araul Logging Area, *Streimann* 13593, 13620 (CBG); Koke Village, *Streimann & Tamba* 11658, 11752 (CBG); Honzeukngon village, *Aptroot* 17826, 17928, 17930, 18019 (Herb. Aptroot); Ekuti Divide, *Streimann* 20164, 20355, 20362 (CBG); Herzog Mountains, *Streimann & Umba* 11113 (CBG); Spreader Divide, *Streimann & Tamba* 11895, 12073, 12208, 12211 (CBG); Slata Creek, *Streimann* 14045 (CBG); Herzog Mountains, *Streimann & Umba* 11134 (CBG); Yinimba, *Streimann* 19712 (CBG); head of Black Cat Creek, *Streimann* 25644 (CBG); Gumi Divide, *Streimann* 22764, 25729 (CBG); **Madang.** Finisterre Range, Teptep Village, *Aptroot* 31931, 32285, 32289, 32290, 32291 (Herb. Aptroot). **Eastern Highlands.** Chimbu. Mt Wilhelm, *Borgmann* 732b, 919 (B); *Aptroot* 18282, 18396, 18528, 18655, 32828, 32834 (Herb. Aptroot); *Kashiwadani* 10880, 10921, 10967, 10998, 11011, 11051, 11062, 11125, 11144, 11312, 11329, 11354 (TNS); *McVean* 66123, 66234, 66254 (CBG); Pindaunde Valley, *Aptroot* 31354, 32742, 33112 (Herb. Aptroot); Toromambuno, *Walker* 8315 (CBG); Lake Piunde, *Sipman* 21985, 22132 (B); Goroka. Mt Zapaliga, 2650 m, *Iserentant* 9546 (Herb. Aptroot); Mt Gahavisuki Provincial Park, *Sipman* 22185 (B); near Mopei Village, *Streimann* 18844 (CBG); Daulo Pass, *Streimann* 18021, 18029, 18077 (CBG). **Western Highlands.** Yobobos, *Hoogland & Schodde* 7639 (B); Kubor Range. Nona River, *Vink* 16473 (Herb. Aptroot); Milep Area, *Vinas* 7644 (CBG); Jimi-Waghi Divide, *Streimann* 22317 (CBG); Kum Magnei Mtn, *Streimann* 20646-7 (CBG); Nebilyer River, *Streimann* 20597 (CBG); Kagamuga, *Streimann* 20429, 21751 (CBG); **Central.** Mt Albert-Edward, *Kashiwadani* 11501, 11758, 11936, 12000 (TNS); 2 km N. of the Waiotape Airstrip, *Kashiwadani* 11657, 12045, 12242 (TNS); Ehu Creek, *Streimann & Naoni* 16615 (CBG); Mt Victoria area, *V. Royen* 10957 (CBG). **Southern Highlands.** Mt Giluwe, *Streimann* 24219 (CBG); Onim Forestry Station, *Streimann* 23592, 24562, 24614, 24631, 24635, 24638, 24640 (CBG); **Enga.** Mape Creek, *Streimann* 22112 (CBG); **Gulf.** Hepataewa, *Streimann* 33845 (CBG). **Solomon Islands:** **Guadalcanal Island.** Mt Gallego, *Hill* 8381 (BM); Mt Popomansiu, *Hill* 9379, 9458, 9625, 9725 (BM). **New Caledonia:** **Noumea.** Mt Koghi, *Hill* 11509 (BM). **Sarramea.** Col

d'Amieu, *Hill* 11884, 11958 (BM). **Norfolk Island:** Selwyn Pine Road, *Streimann* 34663, 34661 (CBG); Mt Pitt, *Streimann* 34817 (CBG); track from Red Road to Mt Bates, *Streimann* 34444 (CBG). **Fiji:** **Viti Levu.** Nadarivatu. District Commissioners House, *Degener* 31814ae,u (B); Nandarivatu, *Green* (BM); Nadala, *Degener* 31807 (B); Mt Nairoso, *Smith* 4100, 4420 (BM). **Samoa:** **Upolu.** *Rechinger* (W); Tutuila, *Reinecke* 62a (BM). **Tahiti:** Fautaua Valley, *Seitchell & Parks* 5442 (BM). **Hawaiian Islands:** **Hawaii.** Mauna Loa, *Rock* [Zahlbruckner: Lich. Rar. Exsic. 171] (BM, B, W); Kipuka Ki, *Degener* 31426 (B); *Weber & Bujakiewicz* (B); Waimea, [ad truncos muscosos in paludosis] *Szatala* [Lichenes Sandwichenses] (B); Glenwood, *Faurie* 938 (BM); Saddle Road, Kipuka, *Smith* 4953 (Herb. Smith). **Kauai.** Sine loco, [on trees] *Heller* (B); Hanapepe River, *Heller* 2630a (BM); Mt Gay summer house, *Faurie* 297 (BM); E. of Kalalau Look-out, *Wedin* 3722 (UPS). **Maui.** Haleakala. Puu Uianiau, 7000 ft, *Degener* 22242 (B); Haleakala National Park, Kalua awa, *Medieros* (Herb. Smith); **Oahu.** Mt Kaala summit, *Degener* 30064 (B); Puu Hapapa near Kolekole Pass, *Doty* (B); Waianae Range, Kaala Natural Area Reserve, *Wedin* 3698 (UPS); Honouliuli Forest Reserve, *Smith* 4125 (Herb. Smith). **Galapagos Islands:** **Isla Sant Cruz.** Academy Bay, *Weber* (COLO); *Horneman* 4/64 (COLO).

7. **Pseudocypbellaria crocatoides** D.J. Galloway in *Graphis Scr.* 5: 8 (1993). Type: Fiji. Taveuni, Mt Utugatau, near summit, tree trunks in rainforest, c. 1140 m, 22 April 1970, *G. Degelius* P-236 (UPS-holotype; BM-isotype). Fig. 8.

Thallus in irregular rosettes or loosely spreading, 4-7(-9) cm diam., loosely attached centrally, margins free and \pm ascending. *Lobes* narrow, 2-5 mm wide, rarely to 10 mm wide, irregularly to complexly branched, \pm imbricate centrally, \pm discrete at margins. *Margins* sinuous or ragged, dentate-incised to \pm richly phyllidiate, slightly thickened below and occasionally also ridged above, occasionally with protruding yellow pseudocypbellae. *Upper surface* dark slate-blue to blue-black when wet, pale glaucous greyish when dry, undulate, matt, smooth, wrinkled to subfaveolate especially at lobe apices, very fragile, friable when dry, pliable when wet. *Phyllidia* common and conspicuous, mainly marginal, very variable, \pm dorsiventral, simple to coralloid-branched, 0.2-1 mm tall (to 3 mm long), fringing lobes with clustered, finger-like proliferations. *Maculae* occasional to frequent, white or pale yellowish, \pm distinctly reticulate, following shallow ridges and in faveolae (\times 10 lens). *Isidia*, pseudocypbellae and soredia absent. *Medulla* white. *Photobiont* cyanobacterial. *Lower surface* pale yellowish white to buff-brown at margins darkening centrally, tomentum pale whitish to grey or buff, to brown-black centrally, rather sparse at margins, thick and entangled centrally. Pseudocypbellae yellow, low-conical, scattered, \pm rounded, 0.1 mm diam. or less, margins only slightly raised, decorticate area flat to convex.

Pycnidia rather sparse, solitary, scattered, at margins and along laminal ridges, ostiole red-brown, punctate-depressed, 0.1 mm diam. or less.

Apothecia very rare, solitary, marginal, sessile, constricted at base, rounded, cupuliform, 1-1.5 mm diam., exciple pale buff or brownish, \pm translucent when wet, coarsely corrugate-scabrid, with a conspicuous, irregularly dentate margin, disc red-brown, slightly roughened and with a thin

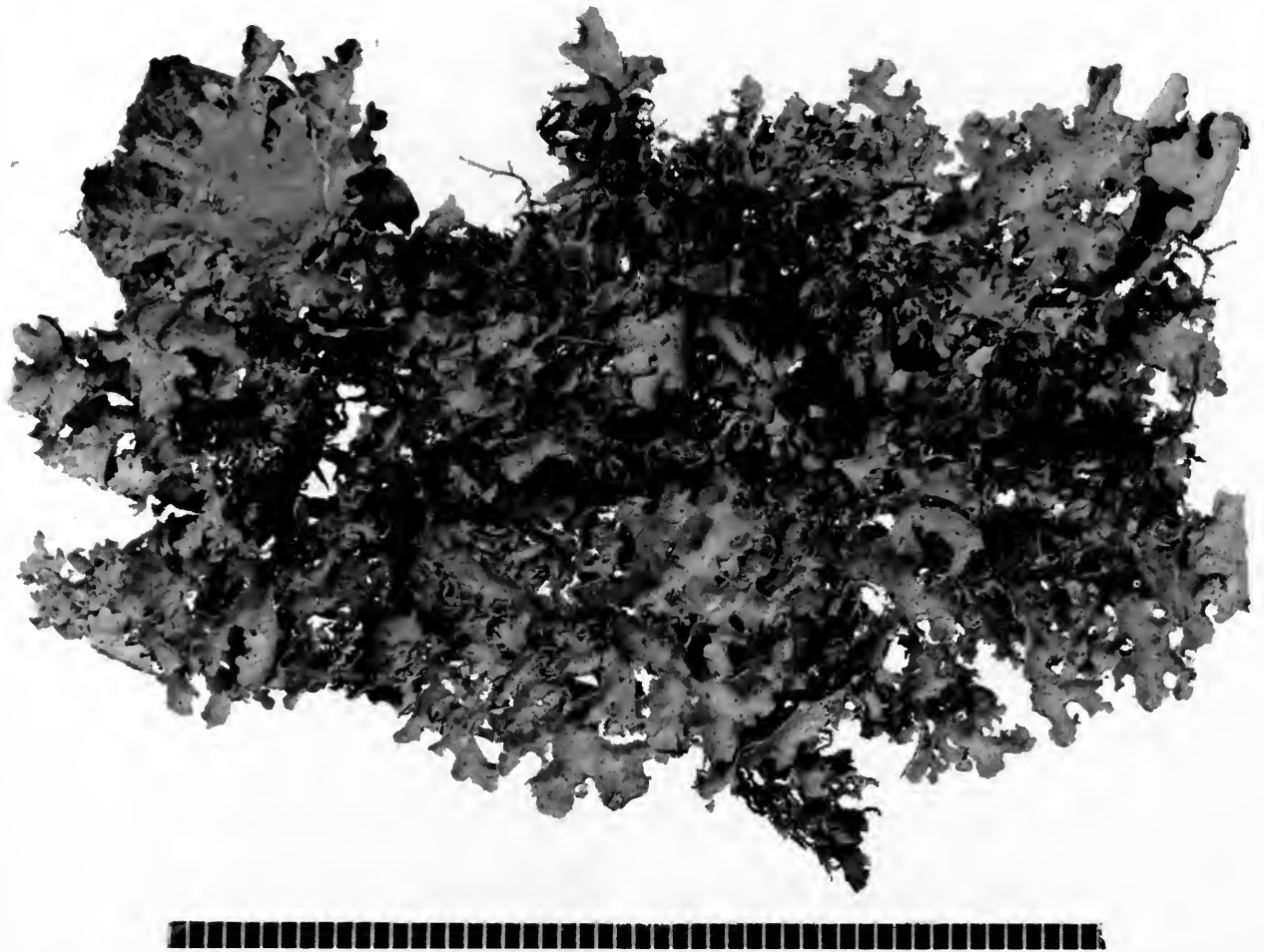


Fig. 8 *Pseudocyphellaria crocatoides*. Isotype (BM). Scale in mm.

white pruina. *Epithecium* 10–14 μm thick, red-brown. *Hymenium* colourless to pale straw, 70–80 μm tall. *Ascospores* not seen.

CHEMISTRY. Pulvinic acid, pulvinic dilactone, 6 α -acetoxyhopane-7 β -22-diol (tr.), 7 β -acetoxyhopane-6 α , 2-diol (tr.), hopane-7 β , 22-diol (tr.), hopane-6 α , 7 β , 22-triol (major), tenuiorin, methyl gyrophorate, gyrophoric acid (tr.), \pm physciosporin (tr.), norstictic (tr.), stictic, cryptostictic, constictic acids.

OBSERVATIONS. *P. crocatoides* is a characteristic species of the *P. crocata* group and has a white medulla, a cyanobacterial photobiont, yellow pseudocyphellae on the lower surface and a chemistry containing stictic acid metabolites, hopane-6 α , 7 β , 22-triol as the dominant triterpenoid, and the pigments calycin, pulvinic acid and pulvinic dilactone (Galloway & Kemp, 1993). It is distinguished by the distinctive marginal (rarely laminal) lobulate proliferations, and a smooth upper surface without isidia or soredia, characters which separate it from *P. crocata* which is yellow-sorediate; from *P. dozyana* which is white-sorediate; from *P. desfontainii* which has terete to squamiform isidia; from *P. neglecta* which has

phyllidia which erode to become pseudosorediate; and from *P. gilva* which has entire margins and is without soredia, isidia, phyllidia or lobulate proliferations.

DISTRIBUTION AND ECOLOGY. Known from Fiji, Papua New Guinea (see below) and also eastern Australia (Fig. 9). Still very poorly collected. Palaeotropical collections so far seen are from humid, shaded, montane rainforest, 840–3000 m.

SPECIMENS EXAMINED. **Fiji:** Taveuni, Mt Utuigatau, *Degelius* P-243 (UPS); Nandarivatu, *Green* (BM). **Papua New Guinea:** Morobe, Mt Kaindi, *Streimann* 17622 (CBG). **Eastern Highlands.** Mt Wilhelm, *Kashiwadani* 10866 (TNS).

8. *Pseudocyphellaria desfontainii* (Delise) Vain., *Résult. Voy. Belgica, Lich.*: 29 (1903). *Sticta desfontainii* Delise in *Mém. Soc. linn. Normandie* 2: 60 pl. 4, fig. 12 (1825). *Stictina carpoloma* f. *desfontainii* (Delise) Nyl. in *Hue, Nouv. Arch. Mus. Hist. nat. Paris* III, 2: 297 (1890). *Sticta carpoloma* f. *desfontainii* (Delise) Zahlbr., *Cat. lich. univ.* 3: 374 (1925). *Cyanisticta desfontainii* (Delise) Räsänen in *Suomal. elain-ja kasvit. Seur. van. kasvit. Julk.* 2(1): 42 (1932), non C.W. Dodge (*Beih. nov. Hedwigia* 12: 173

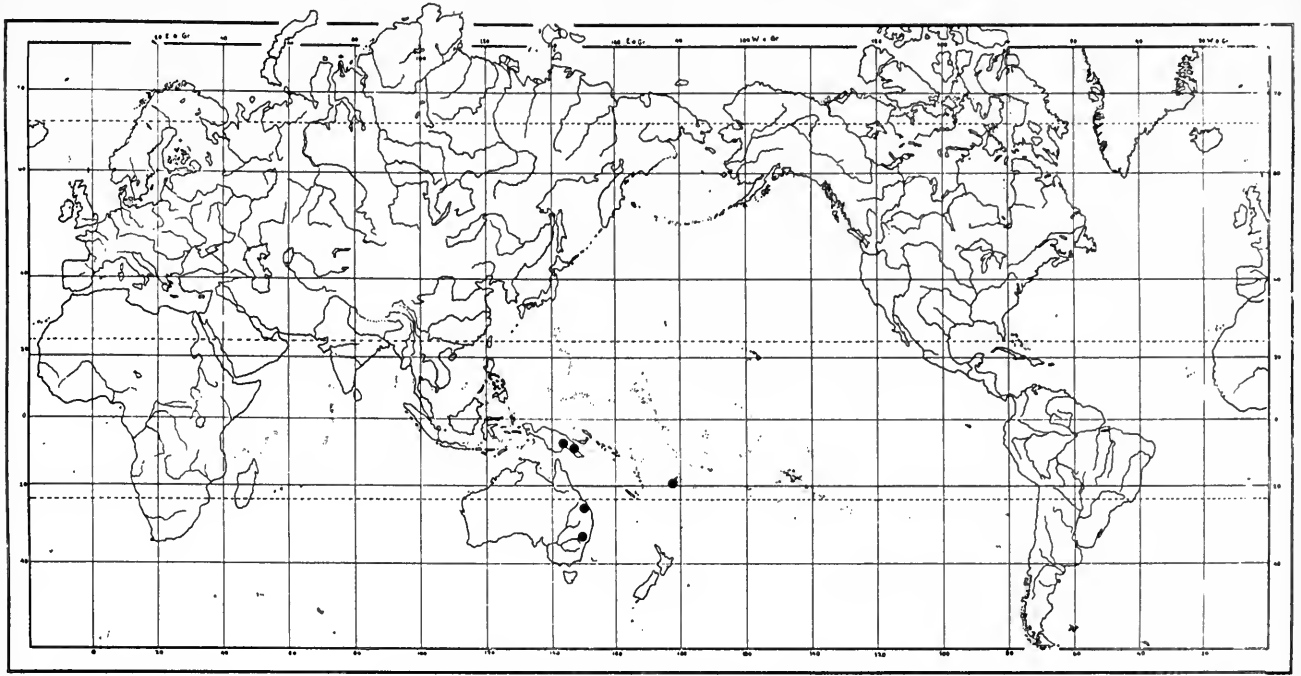


Fig. 9 Distribution of *Pseudocyphellaria crocatoides*.

(1964)). Type: Ile de Bourbon, *Bory de St-Vincent* (PC-THURET-lectotype (Galloway & James, 1986: 434)).

Fig. 10.

Cyanisticta crocata var. *tingaensis* Sbarbaro in *Arch. Bot.* **15**: 102 (1939). Type: Rarotonga, June 1929, *H.E. Parks* (Not seen).

Pseudocyphellaria ceylonensis H. Magn. in *Acta Horti gothoburg.* **14**: 23 (1940). Type: Ceylon [Sri Lanka], Central Province, *G.H.K. Thwaites* 26 (UPS-isotype).

Cyanisticta mougeotiana ssp. *dentata* Räsänen in *Suomal. elain-ja kasvit. Seur. van. Julk.* **20**(3): 16 (1944). Type: New Caledonia, ad corticem arboris, 1863, *E. Vieillard* (H-not seen).

Thallus rosette-forming to irregularly spreading, 4–9(–11) cm diam., closely attached centrally, margins \pm free. *Lobes* 2–8(–15) mm wide, (0.5)1–3(–6) cm long, subdichotomously branching to complex-imbricate, discrete, contiguous or sub-imbricate at margins, complex-imbricate centrally. *Margins* entire in parts (especially at lobe apices) to indented, ragged, incised, crenulate, slightly thickened and ridged below, sparsely to densely isidiate. *Upper surface* dark glaucous blue to blue-black, suffused red-brown towards apices when wet, glaucous grey or pale bluish to red-brown when dry, undulate, shallowly pitted or punctate-impressed to deeply faveolate, ridges sharply defined to smoothly rounded, matt to slightly shining in parts, flabby when wet, brittle and rather fragile when dry, isidia easily broken off leaving yellow scars, without soredia, phyllidia or pseudocyphellae. *Maculae* common, minute, white or yellowish, effigurate to \pm reticulate, best seen when wet (use $\times 10$ lens). *Isidia* sparsely to densely developed, often crowded at margins also on interconnecting ridges or in faveolae, solitary to crowded in groups, terete, simple, rarely squamiform or coralloid, 0.5–1.5 mm tall and 0.1–0.2 mm diam., concolorous with upper surface, eroding

at apices and appearing pseudosorediate, breaking off and leaving yellow scars resembling pseudocyphellae. *Medulla* white, often suffused yellow in upper parts in some collections. *Photobiont* cyanobacterial. *Lower surface* pale yellow-white or buff at margins darkening to red-brown or brown-black centrally, wrinkled-undulate, tomentose from margins to centre or with a narrow, glabrous, marginal zone, tomentum thick and woolly, white to dark brown or \pm blackened. *Pseudocyphellae* yellow, common, scattered, rounded, minute, 0.2 mm diam. or less, rarely 0.5 mm diam., conical-verruciform, decorticate area flat to convex.

Pycnidia laminal, scattered, inconspicuous, slightly swollen, ostiole minute, red-brown to black, 0.1 mm diam. or less.

Apothecia sparse (often absent) to \pm frequent, marginal and laminal 0.5–3 mm diam., sessile, constricted at base to subpedicellate, shallowly to deeply cupuliform, \pm deeply concave to undulate and \pm plane at maturity, exciple prominent, persistent, pale whitish pink, \pm translucent when wet, brownish or red-brown when dry, coarsely corrugate-scabrid, obscuring disc at first, rupturing and leaving an irregular dentate margin, disc red-brown to \pm blackened, grey-white pruinose. *Epithecium* red-brown, 8–14 μ m thick. *Hymenium* colourless to pale straw to pale or dark red-brown, 80–100 μ m tall. *Ascospores* red-brown, ellipsoid, apices pointed, 1-septate, 23–28(–30.5) \times (5.5)–6.5–8.5(–11) μ m.

CHEMISTRY. Tenuoirin, methyl gyrophorate, gyrophoric acid (tr.), hopane-6 α , 7 β , 22-triol, 7 β -acetoxyhopane-6 α , 22-triol (tr.), 6 α -acetoxyhopane-7 β , 22-diol (tr.), stictic, cryptostictic, and constictic acids, pulvinic acid, pulvinic dilactone and calycin.

OBSERVATIONS. *Pseudocyphellaria desfontainii* is characterized by a white medulla; a cyanobacterial photobiont; terete, \pm fingerlike isidia on the upper surface; yellow

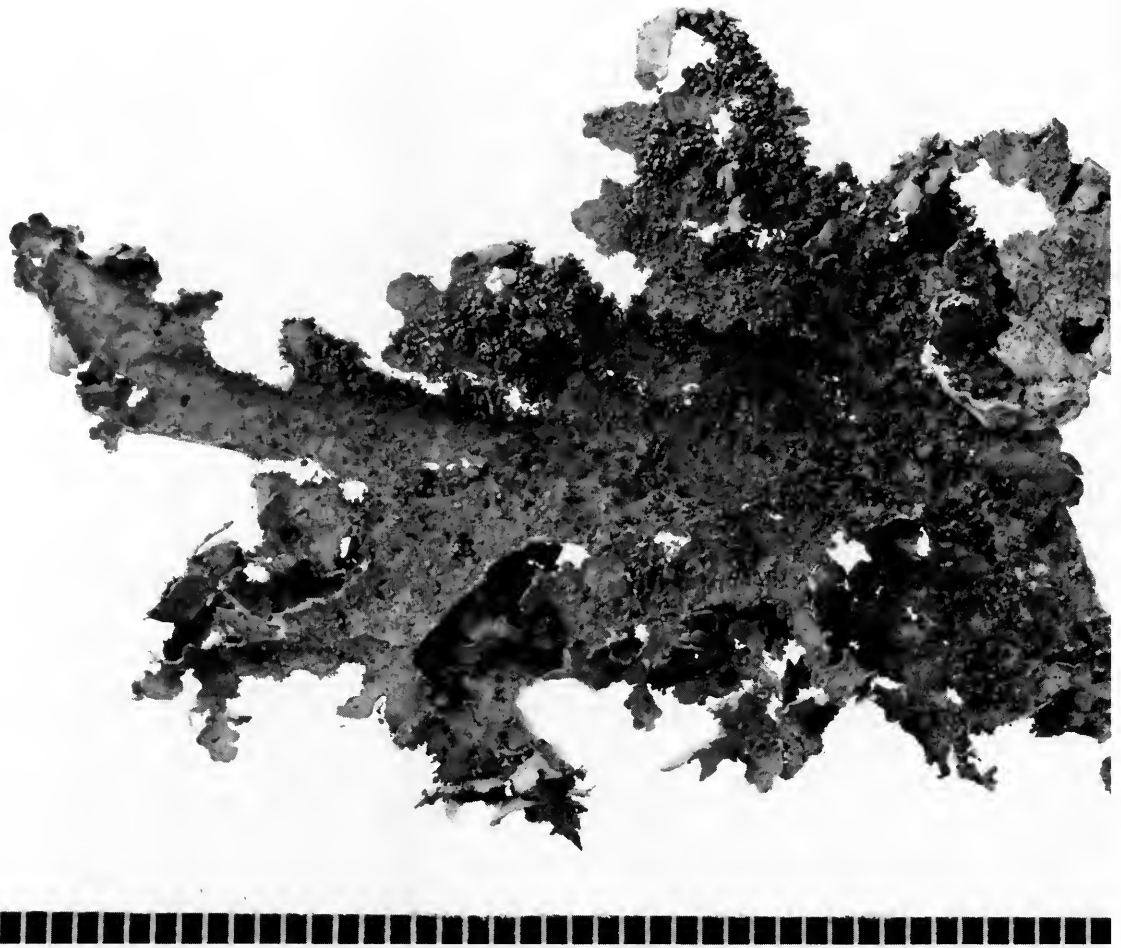


Fig. 10 *Pseudocyphellaria desfontainii*. T.G.A. Green s.n. (BM) Scale in mm.

pseudocyphellae on the lower surface; and a chemistry containing yellow pigments, a dominant hopane-triol and metabolites of the stictic acid aggregate. Its characteristic isidia distinguish it from other members of the *P. crocata* group (see above under *P. crocata* and *P. crocatoides*).

DISTRIBUTION AND ECOLOGY. A strictly palaeotropical taxon (Fig. 11), occurring from Africa to the south-western Pacific eastwards as far as the Marquesas, but not recorded from Hawaii, or the Galapagos Islands (Weber, 1986). On living and dead trees, on rotting logs and on shrubs in montane rainforest, 800–3650 m.

SPECIMENS EXAMINED. **Africa. Tanzania:** Usambara. Amani, *Brunnthaler* (W). **Madagascar:** sine coll. (L-ex Herb Paris); Ambohitombo Forest, *Forsyth Major* 469, 554, 576, 583, 587 (BM). **Mauritius:** sine loco, *McGregor* (BM); Les Mares, *Ouhamed* 8 (BM). **Réunion:** Cirque de Salazie, *K. & A. Kalb* 26562 (Herb. Kalb); zwischen le Brûlé (S von St-Denis) und Plaine des Chicots, *K. & A. Kalb* 26563 (Herb. Kalb); southern slopes of Piton des Neiges, near Cilaos, *Arvidsson & Nilsson* 2539 (GB). **Sri Lanka:** above Pattipola, Horton Plains, *van Steenis* 19924d (L); Mount Pedro, *Blatter* 56 (W);

Nuvara Eliya. Horton Plains, Farr Inn, *Moberg* 2585, 2598 (UPS); Hakgala Botanical Garden, *Lundqvist* 9003 (UPS); Hakgala Botanical Garden, *Degelius* As-411 (UPS); Nuvara Eliya, *Degelius* As-440 (UPS). **Malaysia: Sabah.** Kota Belud, Mt Kinabalu, *Sipman & Tan* 31104 (B). **Pahang.** Fraser's Hill, *Burkill* 2073b, 2796 (L); *Dransfield* 515 (BM); *Degelius* As-611, As-620 (UPS); *Galloway* (KEP); Cameron Highlands, Tanak Rata, *Degelius* As-568, As-576 (UPS). **Indonesia. Java:** Mt Ardjuno, *Groenhart* 1860 (L); Mt Gede, *van Ooststroom* 14592 (L); Cibodas Botanical Garden, *Arvidsson & Nilsson* 2487, 2490, 2497 (GB). **Sulawesi:** Lompo Batang, *Zelf* 250 (L). **Papua New Guinea: Eastern Highlands.** Chimbu. Mt Wilhelm, *Borgmann* 779 (B); *Streimann* 18554 (CBG); *Kashiwadani* 10955, 11044, 11186 (TNS); Goroka. Mt Gahavisuki Provincial Park, *Aptroot* 31036 (Herb. Aptroot); Daulo Pass, *Weber & McVean* (COLO). **Madang.** Finisterre Range. Teptep Village, *Aptroot* 31926, 32287 (Herb. Aptroot). **Morobe.** Kewieng, *Koponen* 34404 (Herb. Aptroot); Mt Kaindi, *Streimann* 17523, 17568, 17602, 17614, 17621, 17663–4 (CBG); *Kashiwadani* 10548 (TNS); *Weber & McVean* (COLO); Upper Watut River, *Streimann* 17078 (CBG); Yinimba, *Streimann* 19061, 19711 (CBG); track to

Mt Missim, Bellamy 206 (CBG); Pouyu Village, Streimann & Tamba 12675 (CBG); logging area 15 km E. of Bulolo, Streimann & Bellamy 13166 (CBG); Gumi Divide, Streimann 22774 (CBG); Wau, Edie Creek Road, Sipman 15627 (Herb. Aptroot); head of Black Cat Creek, Streimann 25653 (CBG). **Central.** 2 km N. of Waiotape Airstrip, Kashiwadani 12242, 12260 (TNS); Mt Albert-Edward, Kashiwadani 11719, 11803 (TNS). **Southern Highlands.** Margarima-Tari Road, Streimann 24394 (CBG); Iaro River, Streimann 23950 (CBG). **Western Highlands.** Karpena plantation N. of Mt Hagen, Streimann 21813, 21825 (CBG); Yobobos, Hoogland & Schodde 7640 (COLO). **Solomon Islands: Guadalcanal Island.** Mt Popomansiu, Hill 9439, 9491, 9575, 9849, 9883 (BM). **New Caledonia: Sarramea.** Col d'Amieu, Hill 12021 (BM). **Fiji: Viti Levu.** Nggaliwana Creek Valley, Smith 5335 (L); N-Baluti trail, Selling (S); Mba, Nandarivatu, Smith 5964 (BM); Nandarivatu, Green (BM). **Taveuni.** Mt Utugatau, Degelius P-205, P-230 (UPS). **Samoa: Upolu.** Lanuto'o, Reching (W). **Tahiti:** Aorai, v. Balgooy (Herb. Aptroot); Onohea Valley, Degelius P-346 (UPS); Belvedere near Papeete, Degelius P-390 (UPS); sine loco, Moseley (BM). **Marquesas Islands: Nukuhiva.** Tovii, Peake (BM).

9. *Pseudocyphellaria insculpta* (Stizenb.) D.J. Galloway in *Lichenologist* 17: 305 (1985). *Stictina insculpta* Stizenb. in *Flora, Jena* 81: 129 (1895). *Stictina impressula* Müll. Arg. in *Flora, Jena* 71: 22 (1888). non Nyl. (*Flora, Jena* 57: 71 (1874), based on *Stictina tomentosa* var. *impressula* Nyl. in *Annls Sci. nat. (Bot.)* V, 7: 305 (1867) from South America). *Sticta insculpta* (Stizenb.) Zahlbr., *Cat. lich. univ.* 3: 388 (1925). Type: Australia. Queensland, Mt Bellenden Ker, Sayer, comm. F. v. Mueller 1887 (G 0020099-holotype).

Fig. 12.

Stictina diplomorpha Müll. Arg. in *Flora, Jena* 65: 301 (1882).

Pseudocyphellaria diplomorpha (Müll. Arg.) D.J. Galloway, *Tropical lichens: their systematics, conservation & ecology*: 9 (1991). Type: Ceylon [Sri Lanka], sine loco, 1876, G.H.K. Thwaites (G 001975-holotype).

Stictina impressula var. *sublaevis* Müll. Arg. in *Hedwigia* 30: 48 (1891). *Stictina insculpta* var. *sublaevis* (Müll. Arg.) Stizenb. in *Flora, Jena* 81: 129 (1895). *Sticta insculpta* var. *sublaevis* (Müll. Arg.) Zahlbr., *Cat. lich. univ.* 3: 388 (1925). Type: Australia. Queensland, Bellenden Ker District, 1889, Bailey 575 pr.p. (G 002105-holotype).

Thallus orbicular to irregularly spreading in entangled clones, 5–12(–20) cm diam., loosely attached centrally, margins and apices free, \pm ascending. *Lobes* very variable, irregularly divided, subdichotomously branching at apices to complex-imbriate centrally, 1–4(–8) mm wide, 0.5–1(–4) cm long. *Margins* irregularly notched or incised, occasionally to densely isidiate or lobulate-phyllidiate. *Upper surface* vivid navy blue to blue-black when wet, olivaceous-grey suffused brownish in parts when dry, irregularly undulate, conspicuously dimpled, punctate-impressed, here and there minutely papillate (use $\times 10$ lens), rather fragile, papery when dry, flabby when wet, isidiate-phyllidiate, maculate, without pseudocyphellae or soredia. *Maculae* frequent, minute, white, effigurate to \pm reticulate imparting a delicate marbling to the upper surface. *Phyllidia* mainly marginal, occasionally also laminal, simple to coralloid, terete to flattened-dorsiventral, constricted at base 0.2–0.5(–1) mm wide, 1–2 mm tall. *Isidia* terete, subgranular at first, becoming flattened-phyllidiate. *Medulla* white. *Photobiont* cyanobacterial. *Lower surface* pale yellow-brown or whitish to buff brown at apices, darkening centrally, glabrous in a narrow to broad marginal zone and tomentose centrally, or uniformly tomentose from margins to centre, tomentum long, silky, white to grey-black or brown-black, densely entangled to \pm felted-woolly. *Pseudocyphellae* prominent, white, round to

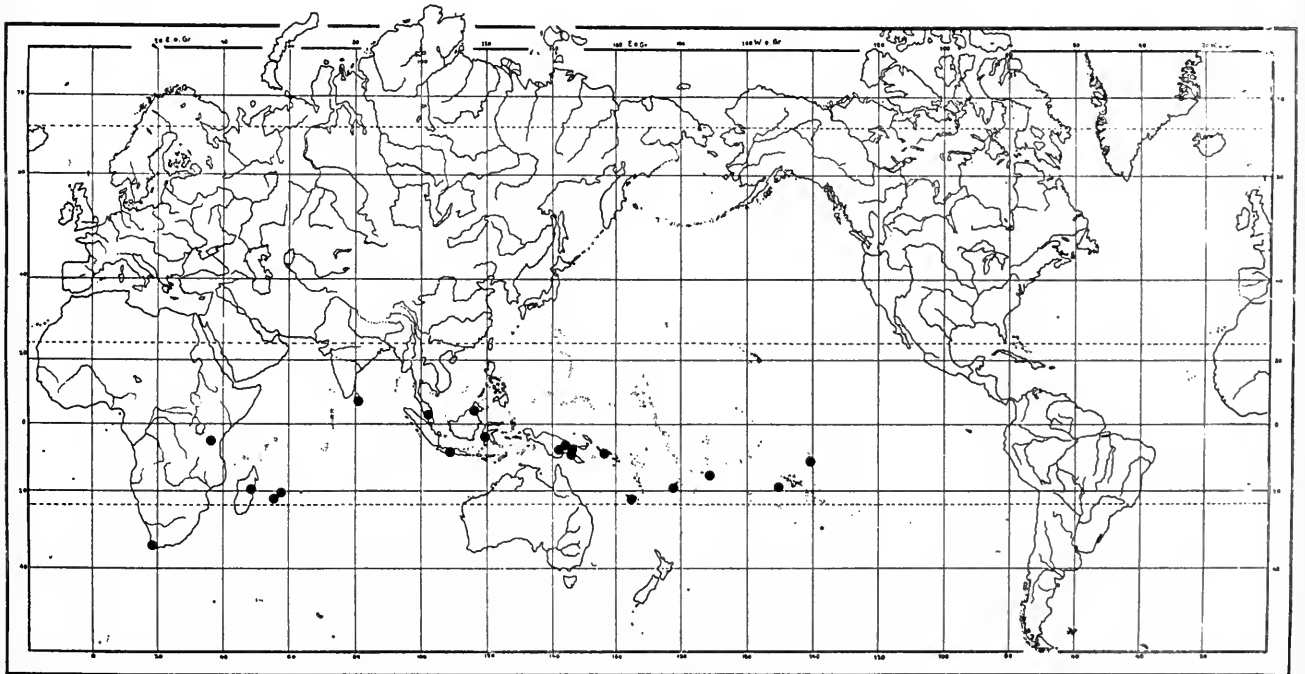


Fig. 11 Distribution of *Pseudocyphellaria desfontainii* in the palaeotropics.

irregular, 0.1–1 mm diam., margins raised, concolorous with lower surface, decorticate area flat to convex, sunk in tomentum.

Apothecia rare or absent to occasional, rounded, 1–2(–2.5) mm diam., sessile, constricted at base to \pm subpedicellate, exciple pale pinkish brown, translucent when wet, wrinkled-striate, with occasional to dense white, silky tomentum below, disc plane to subconcave, red-brown, matt, smooth, epuriose. *Epithecium* pale yellow-brown, 8–12 μ m thick. *Hymenium* colourless, 70–85 μ m tall. *Ascospores* yellow-brown to red-brown 1–3-septate, ellipsoid-fusiform, apices rounded or pointed, 28–33.5 \times 6.5–8.5 μ m.

CHEMISTRY. Methyl gyrophorate, gyrophoric acid, 7 β -acetoxyhopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *Pseudocyphellaria insculpta* is characterized by a white medulla; a cyanobacterial photobiont; projecting marginal lobules or elongate phyllidia; a dimpled to punctate-impressed upper surface; and a two-hopane chemistry with methyl gyrophorate and gyrophoric acid. It is distinguished from *P. prolificans* and *P. multifida*, both of which have

green photobionts; from *P. beccarii* which has entire margins; from *P. argyracea* and *P. dissimilis* which have terete to coralloid isidia; and from *P. crocatoides* which has yellow pseudocyphellae.

DISTRIBUTION AND ECOLOGY. A palaeotropical species known from Sri Lanka to the south-west Pacific (Fig. 13). An epiphyte of trees and shrubs in humid montane rainforest or cloud forest, often growing amongst moss, 300–3760 m.

SPECIMENS EXAMINED. **Sri Lanka:** Big Mount, *Neitner* (US); Adams Peak, *Thor* 391 (S); Horton Plains, World's End, *Bohlin* (S); Central Province, *Thwaites* C11, C22 (BM). **Malaysia:** **Sabah.** Kota Belud. Mt Kinabalu, 1650–3100 m, *Sipman & Tan* 31075, 31383 (B). **Indonesia.** **Sumatra:** ?Gunung Leuser National Park, *Assink* s.n. (Herb. Aptroot). **Java:** Malang, *Lederer* s.n. (B); Tjibodas. Mt Gede, *Schiffner* 3079 (L); sine loco, *Zollinger* (L); Mt Ardjuno, *Groenhart* 7328 (L). **Philippines:** **Luzon.** Benguet. Mt Santo Tomas, *Sipman* 21819 (B); sine loco, *Loher* (BM). **Papua New Guinea:** **Eastern Highlands.** Chimbu. Mt Wilhelm, *Borgmann* 821 (B); *Aptroot* 32880 (Herb. Aptroot); *Kashiwadani* 10843, 10861, 10865, 10912, 10952, 11045, 11450 (TNS); Bundi Gap,

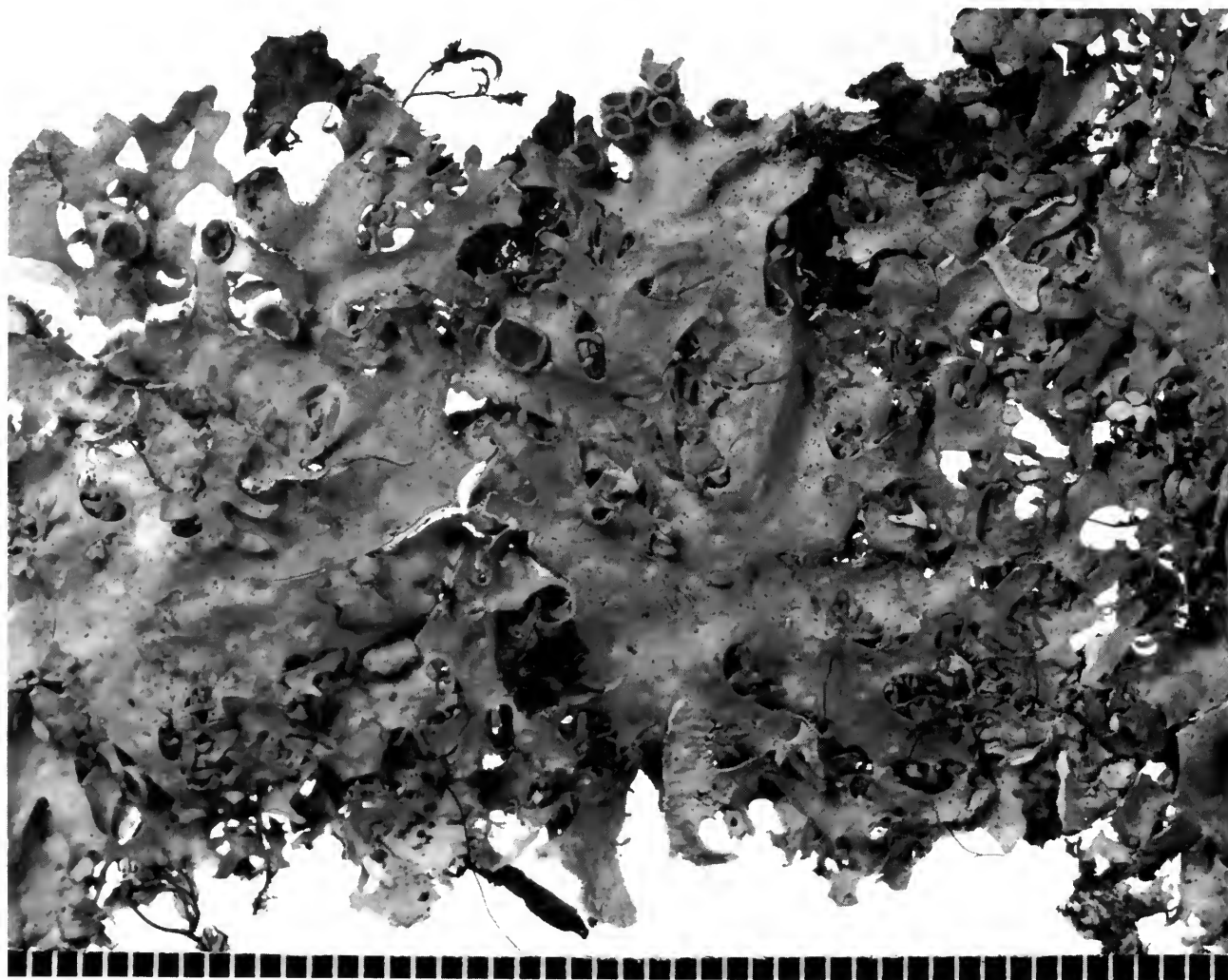


Fig. 12 *Pseudocyphellaria insculpta*. G. Thor 391 (S). Scale in mm.

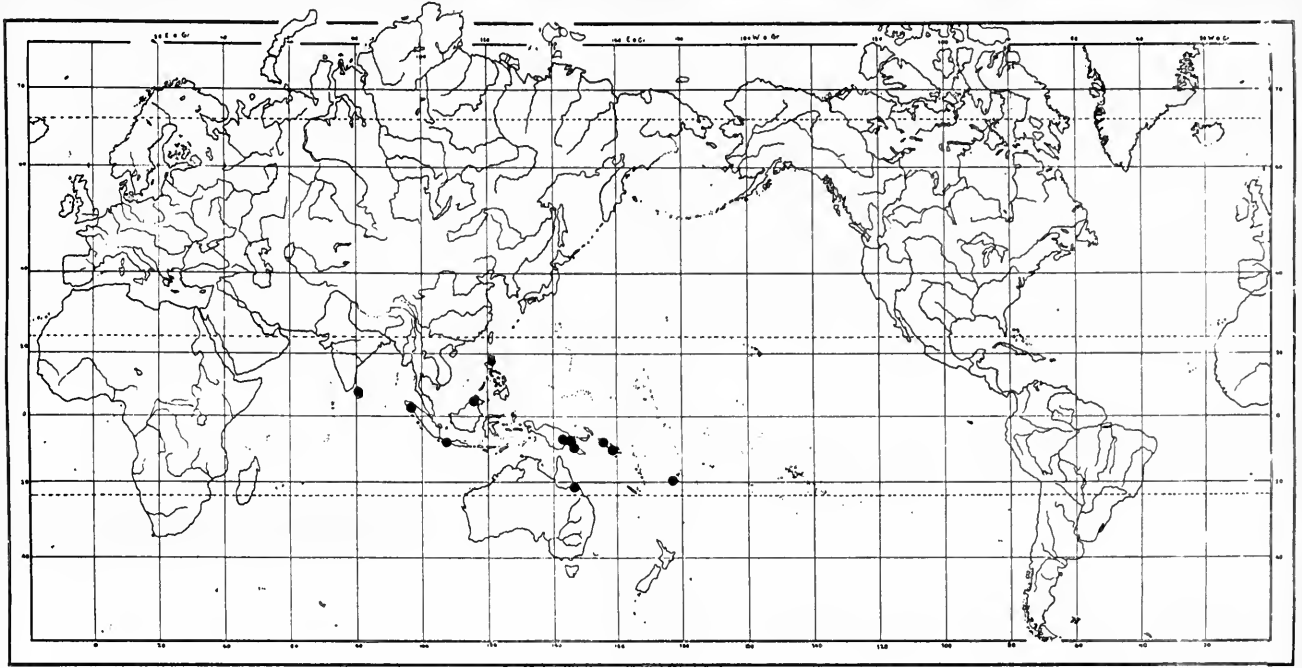


Fig. 13 Distribution of *Pseudocyphellaria insculpta* in the palaeotropics.

Aptroot 32197 (Herb. Aptroot); Pindaunde Valley, *Aptroot* 32741 (Herb. Aptroot). **Morobe.** Cromwell Mountains. Siwea, *Koponen* 30489 (Herb. Aptroot); track to Mt Missim, *Bellamy* 210a,c (CBG); Kaisinik, *Kashiwadani* 10738 (TNS); Mt Kaindi, *Streimann* 33207 (CBG). **Central.** Mt Albert-Edward, *Kashiwadani* 11807 (TNS); 2 km N. of Waiotape Airstrip, *Kashiwadani* 12263 (TNS). **Southern Highlands.** Onim Forestry Station, *Streimann* 24627 (CBG). **Solomon Islands: Guadalcanal Island.** Mt Popomansiu, *Hill* 9289, 9315, 9383, 9432, 9435, 9495–6, 9512, 9559–60, 9667 (BM). **Kolombangara Island.** South Summit, *Hill* 10494 (BM). **Fiji: Viti Levu.** Mba, immediate vicinity of Nandarivatu, *Smith* 5964 (US).

10. *Pseudocyphellaria dissimilis* (Nyl.) D.J. Galloway & P. James in *Lichenologist* 12: 297 (1980). *Stictina fragillima* var. *dissimilis* Nyl., *Syn. meth. lich.* 1(2): 336 (1860). *Stictina dissimilis* (Nyl.) Nyl. in *J. Linn. Soc. Lond.* 9: 246 (1866). *Sticta fragillima* var. *dissimilis* (Nyl.) Kremp., *Reise Ost Freg. Novara Bot.* 1: 119 (1870). *Cyanisticta dissimilis* (Nyl.) Räsänen in *J. Jap. Bot.* 16: 143 (1940). Type: Australia. Sine loco, *Hampe* (H-NYL 34103-lectotype (Galloway & James, 1980: 297)).

Pseudocyphellaria dissimilis is dark slate-blue to blue-black when wet, pale greyish to buff when dry; it is a characteristic isidiate palaeotropical species with a white medulla and white pseudocyphellae on the lower surface which is described in detail in Galloway (1988: 122–126).

CHEMISTRY. Gyrophoric acid (tr.), 7 β -acetoxyhopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *Pseudocyphellaria dissimilis* is a highly variable palaeotropical species having linear-elongate to shallowly rounded, subdichotomously to irregularly branched lobes, often \pm canaliculate and with entire margins becoming

isidiate or occasionally also phyllidiate. The upper surface is smooth or shallowly wrinkled, glossy or matt, minutely maculate and papillate ($\times 10$ lens), and with laminal and marginal isidia, and/or phyllidia. Isidia are simple, \pm terete at first and later may become coralloid-branched or flattened and \pm phyllidiate. It has a white medulla, a cyanobacterial photobiont, and a pale to brownish often \pm costate lower surface with rather sparse, short central tomentum and scattered, fleck-like pseudocyphellae. Spores are pale yellow-brown, 1–3-septate, straight or slightly curved, apices rounded or pointed, 20.5–29.5 \times 7–9 μ m. It has a basic two-hopane chemistry (Wilkins, 1993) with or without traces of gyrophoric acid. Its physiology is discussed in Green et al. (1991) and Lange et al. (1993). It is distinguished from *P. insculpta* in lacking a punctate-impressed upper surface; from *P. argyracea* in lacking laminal pseudocyphellae associated with isidia; from *P. desfontainii* which has yellow pseudocyphellae and a different chemistry; and from *P. crocatoides* which has marginal and laminal proliferations, yellow pseudocyphellae and a different chemistry.

DISTRIBUTION AND ECOLOGY. Apparently rather rare in the palaeotropics where it has to date been positively identified only from Papua New Guinea and Norfolk Island collections from montane rainforest. It is common in north-eastern Australia and throughout New Zealand (Galloway, 1988) and is also recorded from Juan Fernandez but not from continental South America (Galloway, 1992).

SPECIMENS EXAMINED. **Papua New Guinea: Eastern Highlands.** Goroka. Mt Zapaliga, *Iserentant* 9534 (Herb. Aptroot). **Norfolk Island:** sine loco, sine coll. (MEL).

11. *Pseudocyphellaria dozyana* (Mont. & Bosch) D.J. Galloway in *Lichenologist* 17: 304 (1985). *Sticta dozyana* Mont. & Bosch, *Syll. gen. sp. crypt.*: 326 (1856). *Stictina dozyana* (Mont. & Bosch) Nyl., *Syn. meth. lich.* 1(2): 335 (1860).

Saccardo dozyana (Mont. & Bosch) Trevis., *Lichenotheca veneta* exs. no. 75 (1869). Type: Java, without specific locality or date of collection, *Junghuhn* (L 910,215-1471-lectotype (Galloway & Arvidsson, 1990: 128)).

NOTE. Material in PC-HUE is similar in all respects to the Leiden specimen, both are fertile having young, immature, marginal fruits and obviously represent parts of the same collection. The Paris material has a printed label 'Herbarium R.B. van den Bosch' and is further labelled in van den Bosch's hand 'Sticta intricata Del. Java Junghuhn', to which Montagne has added 'Sticta Dozyana M. et V.d.B.'.

Stictina mougeotiana var. *albocyphellata* Nyl., *Syn. meth. lich.* 1(2): 341. 1860. Type: Ins Bourbonia [Réunion], without specific locality, collector or date (H-NYL 33995-holotype).

Pseudocyphellaria dozyana belongs to the *P. crocata* group (white medulla, cyanobacterial photobiont and a chemistry dominated by stictic acid metabolites and hopane-6 α , 7 β , 22-triol) and has a punctate-impressed to faveolate upper surface with characteristic white marginal soralia with a pale yellow tinge to the exposed medulla beneath the white soralia.

CHEMISTRY. Tenuiorin, methyl gyrophorate, hopane-6 α , 7 β , 22-triol, stictic, constictic, cryptostictic acids and traces of unidentified triterpenes.

OBSERVATIONS. *Pseudocyphellaria dozyana* is dark slate-blue to blue-black when wet, pale glaucous-greyish when dry; it has a white medulla, a cyanobacterial photobiont, white pseudocyphellae on the lower surface (rarely these may be pale yellowish at margins), and conspicuous, sinuous, marginal soralia containing grey-white, granular soredia often eroding faint yellowish below. Lobes are broadly elongate-laciniate and are conspicuously punctate-impressed to faveo-

late. The broadly elongate-laciniate lobes and the prominent punctate-impressed to faveolate upper surface, the white marginal soralia and the mainly white pseudocyphellae distinguish this species from *P. crocata* which has prominent yellow soralia and yellow pseudocyphellae, and from *P. bartlettii* which has broadly rounded, \pm rosette-forming lobes with reticulate soralia. *P. intricata* has a smooth upper surface with scattered laminal and marginal soralia which never erode yellowish below, and its chemistry is different, having two hopane-diol triterpenoids and lacking the stictic acid complex of metabolites. Montagne & van den Bosch's record of *Sticta granulata* from Java (Montagne & van den Bosch, 1857: 437-438) evidently refers to *P. dozyana* (Groenhart, 1936).

DISTRIBUTION AND ECOLOGY. A palaeotropical species ranging from the Uluguru Mountains in East Africa and Madagascar and Réunion in the Indian Ocean to the Galapagos Islands (Weber, 1993) in the eastern Pacific (Fig. 14). Known also from Ecuador (Galloway & Arvidsson, 1990). On living and dead trees and shrubs in humid primary and secondary rainforest, 550-2000 m.

SPECIMENS EXAMINED. **Africa. Tanzania:** Uluguru Mountains, Mindu Hill near Morogoro, *Pocs & Ochyra* 88102/AO (BM). **Madagascar:** near Aulanarin, *Pool* (BM). **Réunion:** Cirque de Cilaos: Aufsteig von der Strasse zwischen Cilaos und Ilet a Cordes aud den Col du Taibit, *K. & A. Kalb* 26565, 26566 (Herb. Kalb); Piton des Neiges, 1500 m, *Arvidsson & Nilsson* (GB). **Indonesia. Sulawesi.** Sine loco, Herb. Lugd. Batav. (L); Monado, *Quindal* (M). **Java.** Sine loco, *Junghuhn* s.n. (L); Mt Merbabu, *Surjanto* 1608 (L); sine loco, *Junghuhn* (L); Mt Gede, *Schiffner* 1149 (L); sine loco, sine coll. (H-NYL 34070, 34072). **Papua New Guinea: Eastern Highlands.** Goroka. Lutheran Guesthouse, *Sipman* 22324 (B). **Central.** Near Dabamura, 40 km NE of Port Moresby, *Streimann & Naoni* 14957 (CBG). **Morobe.** Herzog Mountain, *Streimann & Umba* 11050 (CBG). **Western Highlands.**

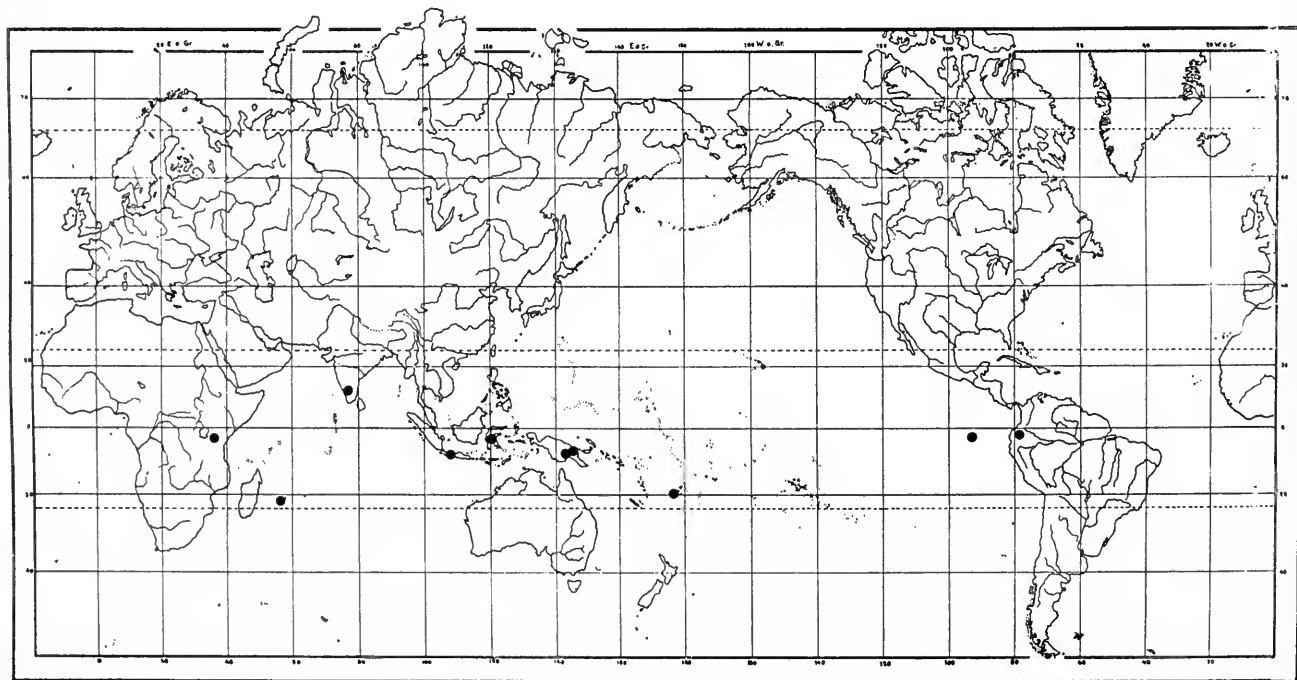


Fig. 14 Distribution of *Pseudocyphellaria dozyana* in the palaeotropics.

Baiyer River Sanctuary, *Streimann* 21042 (CBG); Kagamuga, *Streimann* 24787 (CBG). **Fiji:** *Viti Levu*. Mba, slopes of Mt Nairoso, eastern flank of Mt Evans Range. *Smith* 4100 (US). **Galapagos Islands:** *Isla Santa Cruz*. Table Mt, *Weber* 288 (COLO). *Isla Santiago*. Above James Bay, *Pike* 2732 (COLO). *Isla Charles*. *Weber* 443 (COLO); trail from Black Beach to highlands, *Weber & Lamer* (COLO).

12. *Pseudocyphellaria gilva* (Ach.) Malme in *Bih. K. svenska Vetenskakad. Handl.* 25(3/6): 32 (1899). *Lichen gilvus* Ach., *Lichenogr. succ. prod.*: 157 (1799) [‘1798’]. *Sticta gilva* (Ach.) Ach., *Methodus*: 278 (1803). *Sticta crocata* var. *gilva* (Ach.) Ach., *Syn. meth. lich.*: 232 (1814). *Stictina gilva* (Ach.) Nyl., *Syn. meth. lich.* 1(2): 339 (1860). *Saccardoia gilva* (Ach.) Trevis., *Lichenotheca Veneta* exs. 75 (1869). *Cyanisticta gilva* (Ach.) Gyeln. in *Reprrium Spec. nov. Regni veg.* 29: 5 (1931). Type: [South Africa] Cap.b.Spei, *Thunberg* (UPS-THUNBERG 26816-lectotype (Galloway, 1992: 130)).

Cyanisticta gilva var. *lanata* (Pers.) Gyeln. in *Reprrium Spec. nov. Regni veg.* 29: 5 (1931). *Collema lanata* Pers. in *Gaudich., Voy. Uranie*: 204 (1827). Type: In insulis Maclovianis [Falkland Is], *Gaudichaud* (?PC-not seen).

Cyanisticta gilva var. *pseudogilva* Gyeln. in *Reprrium Spec. nov. Regni veg.* 29: 6 (1931). Type: South Africa ‘Promontorium Bonae Spei’, *Gueinzus* (B-holotype).

Cyanisticta gilva var. *philippiana* Gyeln. in *Reprrium Spec. nov. Regni veg.* 29: 6 (1931). Type: Philippines. Luzon, Benguet Subprovince, May 1911, *E.D. Merrill* 7962 (B-holotype; B-isotype).

Pseudocyphellaria lombokensis H. Magn. in *Acta Horti gothoburg.* 14: 26 (1940). Type: [Java] East India. Lombok, Goenoeng Rindjani, 1925, *T.Å. Tengvall* (?UPS- not seen).

Pseudocyphellaria gilva described originally from Table Mountain at the Cape of Good Hope in the eighteenth century (Galloway, 1992) is a palaeotropical species in the *P. crocata* complex of taxa, having a white medulla, a cyanobacterial photobiont, yellow pseudocyphellae on the lower surface and hopane-6 α , 7 β , 22-triol as the principal terpenoid present in the medulla. Spores are red-brown, 1–3-septate, fusiform-ellipsoid, apices pointed, 22–30 \times 9–11 μ m. The species is described in detail in Galloway (1992: 130–135).

CHEMISTRY. Tenuiorin, methyl gyrophorate, hopane-6 α , 7 β , 22-triol, stictic, cryptostictic, constictic, salazinic (tr.) and norstictic (tr.) acids, calycin, pulvinic acid and pulvinic dilactone.

OBSERVATIONS. *Pseudocyphellaria gilva* is livid slate-blue suffused red-brown in parts when wet, pale grey-brown, olivaceous-brown to brown-black when dry; it has a white medulla; a cyanobacterial photobiont; irregularly branching to imbricate lobes with \pm subdichotomously branching apices, entire margins often with conspicuous, yellow pseudocyphellae; a glossy, undulate to subfaveolate upper surface, lacking soredia, isidia, maculae or phylidia; a dark red-brown to black lower surface with conspicuous, conical-verruciform, yellow pseudocyphellae; apothecia are rare to frequent, young fruits with a characteristic red-ochre margin to the disc which may sometimes be slightly grey-pruinose. It shows a wide range of variation throughout its range (Galloway, 1992: 133). It is distinguished from *P. crocata* by lacking

soredia; from *P. crocatoides* in the thicker, darker thallus and the absence of marginal proliferations; from *P. desfontainii* in the absence of isidia; from *P. beccarii* in having a cyanobacterial photobiont, yellow pseudocyphellae and a different chemistry. The palaeotropical taxon with which it has been confused (see Magnusson, 1940), *P. carpoloma*, has a green photobiont, much more divergent, dichotomously branching lobes and a different chemistry (Code D of Wilkins & James (1979)).

DISTRIBUTION AND ECOLOGY. A palaeotropical species (Fig. 15) ranging from South Africa (the type locality is Table Mountain) through the south-west Pacific tropics to southern South America (Galloway, 1992). On trees and shrubs, amongst mosses and overgrowing rocks in humid montane forest or cloud forest, 250–3600 m. Also in eastern Australia from Queensland to Tasmania.

SPECIMENS EXAMINED. **Africa. South Africa:** Kirstenbosch, *Almborn* [Lichenes africans 9] (BM, L); Table Mt, *Garside* (L); *Sipman* 20.165, 20.194 (B); *Eaton* (BM); *McGillivray* (BM); Simon’s Bay, *Wright* (BM); Cape, *Drège* (BM). **Mauritius:** sine loco, *Blackburn* (BM). **Malaysia: Sabah.** Mt Kinabalu, *Samsudin* (UKMB). **Indonesia. Java:** sine loco. *Horsfield* (BM); Mt Ardjuno, *Groenhart* 26, 32, 42, 1857, 1858, 1871 (L); Mt Kawi/Mt Panderman, *Groenhart* 1825, 1956, 7262, 7263, 7264, (L); Mt Merbabu, *Surjanto* 1612 (L); Tjemorokandang, *Groenhart* 7261 (L). **Philippines: Luzon.** Benguet, Pauai, 2100 m, *McGregor* 8528 (B); *Merrill* 7962, 7972 (BM); Mt Santo Tomas, *Sipman* 21777d (B); *Aptroot* 20358 (Herb. Aptroot); *Degelius* As-854, As-876 (UPS). **Mindanao.** Mt Apo, *Copeland* 1089, 1092 (B, MEL). **Papua New Guinea: Eastern Highlands.** Chimbu. Mt Wilhelm, *Weber & McVean* (B, COLO); *Aptroot* 18211, 32828 (Herb. Aptroot); *Borgmann* 756, 934, 936 (B); *Kashiwadani* 10883, 10916, 10965, 10975, 10980, 10997, 11095, 11127, 11291, 11400, 11404, 11428, 11467 (TNS); *McVean* 6699, 66189 (CBG); *Wade* 8065 (COLO); *Weber* [Lich. Exs. 373] (BM); Pindaunde Valley, *Sipman* 15908, 21988 (B); Bundi Gap, *Aptroot* 32550; Kombugomambuno, *Mundua* 139 (CBG); 2 km N. of Chimbu Airstrip, *Kashiwadani* 12432 (TNS); Lake Aunde, *Aptroot* 18462, 18477 (Herb. Aptroot); Goroka. Mt Gahavisuki Provincial Park, 2400 m, *Aptroot* 31029, 31140 (Herb. Aptroot); *Streimann* 18204 (CBG); *Sipman* 22193 (B); Daulo Pass, *Hoffmann* 89–441 (Herb. Aptroot); *Streimann* 17968, 18080, 18116 (CBG); Wopeia. Near Aiyura, *Streimann* 18328 (B); track to Mt Michael, *Streimann* 18475 (CBG); near Hogabi Village, *Streimann & Bellamy* 18687 (CBG); Kassam Pass, *Streimann & Umba* 11427–8, 11504 (CBG). **Morobe.** Saruwaged, *Sipman* 24385 (B); Mt Sarawaket [Saruwaged] Southern Range, *Koponen* 32731 (Herb. Aptroot); Hekwangi Village, *Streimann* 19362 (B); track to Mt Missim, *Bellamy* 210a.c (CBG); Upper Watut River, *Streimann* 17179, 17239 (CBG); Mt Kaindi, *Streimann & Bellamy* 17675, 19875 (CBG); *Streimann* 22495, 22510 (CBG); Yakwoi River, *Streimann* 19261 (CBG); Rawlinson Range, *Strong Clemens* 12444 (COLO); Pouyu Village, *Streimann & Tamba* 12712 (CBG); Ekuti Divide, *Streimann* 20173, 24932 (CBG); head of Black Cat Creek, *Streimann* 25643, 25646–7 (CBG); Logging Area 15 km W. of Bulolo, *Streimann & Bellamy* 13142 (CBG); near Hunzeukngon Village, *Aptroot* 18023 (Herb. Aptroot); Gumi Divide, *Streimann* 25062 (CBG). **Western Highlands.** Mt Karoma, *Veldkamp & Wiakabu* (Herb. Aptroot); Baiyer River Sanctuary,

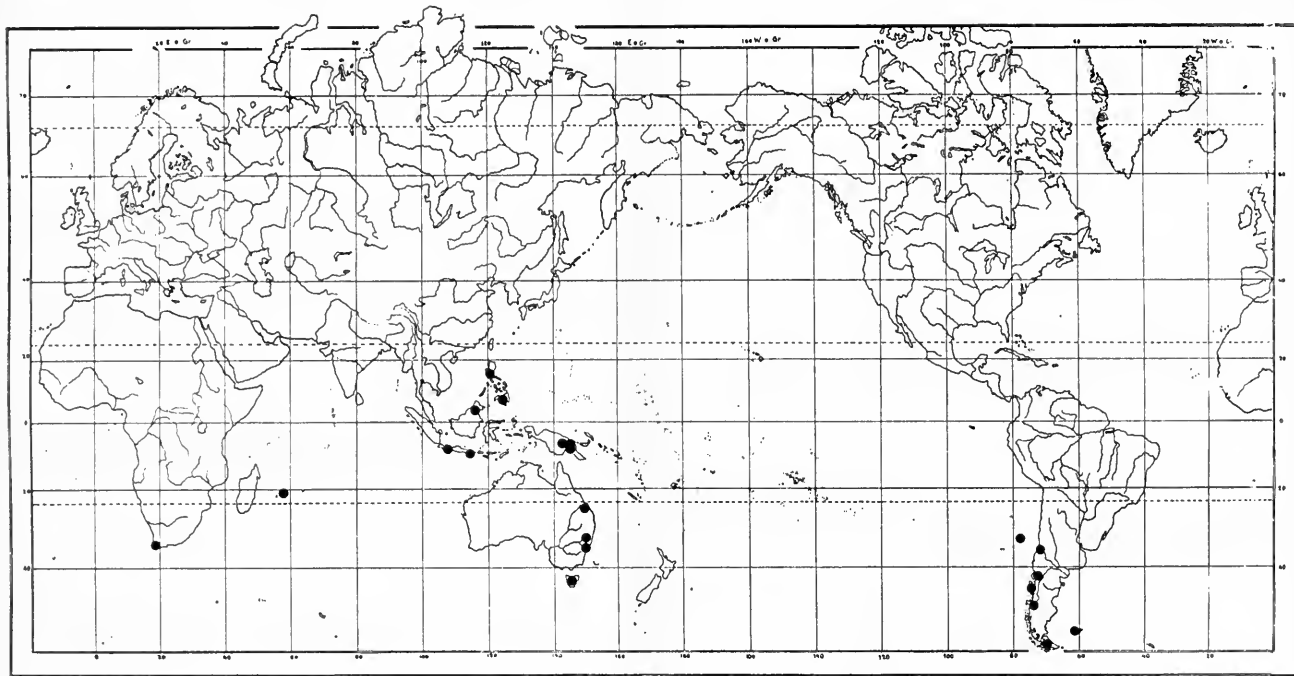


Fig. 15 Distribution of *Pseudocyphellaria gilva* in the palaeotropics.

Streimann 21116 (CBG); Tumbang Village, *Streimann* 21361 (CBG); Mur Mur Pass, *Streimann* 21174 (CBG). **Madang.** Finisterre Range, Teptep Village, *Aptroot* 31982, 31992, 32292, 32294 (Herb. Aptroot). **Southern Highlands.** Lai River, *Streimann* 22213, 22216 (CBG); Iaro River, *Streimann* 23827, 23837 (CBG); Munia Logging Area, *Streimann* 23320, 23325, 23666 (CBG); Lama Sawmill Logging Area, *Streimann* 24690 (CBG); Paunde Logging Area, *Streimann* 23346, 23354 (CBG). **Enga.** Mape Creek, *Streimann* 21555 (CBG).

13. ***Pseudocyphellaria godeffroyi*** (Kremp.) D.J. Galloway in *Lichenologist* 17: 304 (1985). *Sticta* (*Stictina*) *godeffroyi* Kremp. in *J. Mus. Godeffroy* 1(4): 99, tab. 14 fig. 10 (1874). Type: Fiji, Viti Levu, Noggara, *Dr E. Gräffe* 67 (M-lectotype (Galloway, 1985: 304)).

Fig. 16.

Stictina intricata var. *gymnoloma* Nyl., *Syn. meth. lich.* 1(2): 335 (1860). Type: Fidji insulae, *Milne* (H-NYL 34090-lectotype (Galloway, 1985: 304)).

Thallus rosette-forming, wide-spreading, 5–12(–25) cm diam., closely attached centrally, margins \pm free. **Lobes** broadly rounded, 8–15(–20) mm diam., contiguous to overlapping at margins, imbricate centrally. **Margins** entire, sinuous, shallowly to deeply notched, slightly thickened. **Upper surface** dark glaucous blue to dark malachite green-blue, suffused brownish at apices when wet, pale buff brown or red-brown to pale cinnamon brown when dry, undulate, irregularly pitted or shallowly wrinkled in places, minutely roughened to verrucose-scabrid, scabrosity best seen at lobe apices (use $\times 10$ lens), apices minutely white-tomentose, coriaceous, tough when dry, pliable, flabby when wet, pseudocyphellate, without isidia, phylidia or soredia. **Pseudocyphellae** white, round to irregular, scattered, occa-

sional to frequent, 0.2–1.5 mm diam., large prominent pseudocyphellae \pm ulcerose with a raised margin, decorticate area flat to concave. **Medulla** white. **Photobiont** cyanobacterial. **Lower surface** pale yellowish buff or brownish at margins, darkening centrally, uniformly short velvety tomentose, tomentum very even, pale buff to dark red-brown. **Pseudocyphellae** white, prominent, scattered, often crowded, minute, at margins 0.1–0.3 mm diam., larger centrally, round to irregular, 1–2 mm diam., margins very shallowly raised, concolorous with lower cortex, decorticate area flat to concave, distinctly granular-roughened.

Pycnidia prominent, solitary or crowded, marginal and laminal, raised, to 0.5 mm diam., hemispherical, ostiole red-brown, 0.1–0.2 mm diam.

Apothecia sparse to frequent, often crowded at centre of thallus, rare at margins and lobe apices, sessile, constricted at base, round to irregular-deformed through mutual pressure, 1–3 mm diam., exciple prominent, persistent, pale brownish, conspicuously verrucose-scabrid forming a distinctive corrugate-scabrid margin to disc, disc concave to plane, pale to dark red-brown, shining, epruinose. **Epithecium** pale red-brown, 14–22 μm thick. **Hymenium** colourless to pale straw, 80–95 μm tall. **Ascospores** 1–3-septate, pale yellow-brown to red-brown, fusiform-ellipsoid, apices rounded or pointed, straight or curved, 28–33.5 \times (5.5–)6.5–8.5(–11) μm .

CHEMISTRY. 7 β -acetoxyhopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *Pseudocyphellaria godeffroyi* is characterized by a white medulla, white pseudocyphellae on both upper and lower surfaces, a cyanobacterial photobiont, and broad rounded lobes with a distinctive-scabrid-areolate upper surface. It is distinguished from *P. punctillaris* which has a scabrid-areolate upper surface and isidia or lobules at the margins; from *P. rigida* which has a scrobiculate upper

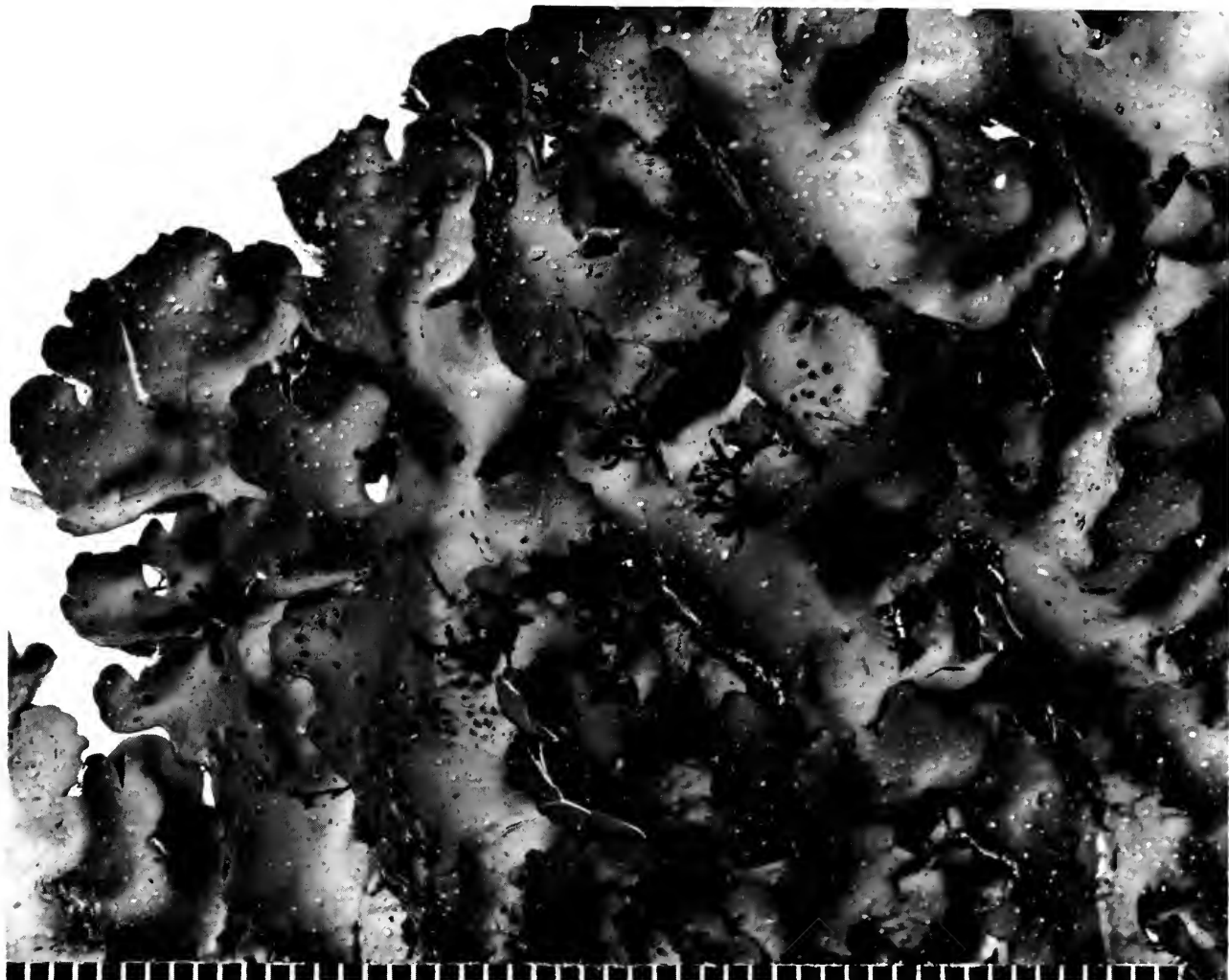


Fig. 16 *Pseudocypbellaria godeffroyii*. T.G.A. Green s.n. (BM). Scale in mm.

surface (not areolate-scabrid); from *P. semilanata* which has a smooth, not areolate-scabrid upper surface; and from *P. trichophora* which has a smooth upper surface and distinctive tomentose-hairy lobe margins.

DISTRIBUTION AND ECOLOGY. Apparently restricted to Fiji where it occurs on trees in open slopes and on trees and scrub in humid, montane rainforest, 700–1100 m.

SPECIMENS EXAMINED. **Fiji:** Viti Levu. Sine loco, Milne (BM); Mba, Nandarivatu, Smith 5963 (BM); Nandarivatu, Green (BM); Naggarra, Graeffe 64, 69 (M).

14. ***Pseudocypbellaria haywardiorum*** D.J. Galloway in *Bull. Br. Mus. nat. Hist. (Bot.)* 17: 159 (1988). Type: New Zealand. North Island, South Auckland, Red Mercury Island, on tea tree (*Leptospermum*) bark, August 1971, B.W. & G.C. Hayward H 40.4 (AK 161261-holotype).

Pseudocypbellaria haywardiorum is a palaeotropical species of rather limited distribution in the South Pacific. It is discussed in detail in Galloway (1988: 159–162) and in Elix et al. (1992).

CHEMISTRY. 7 β -acetoxyhopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *Pseudocypbellaria haywardiorum* is a palaeotropical sorediate species having \pm rounded to irregularly lacinate lobes with coarsely granular to pseudoisidiate ($\times 10$ lens) laminal and marginal soralia, and a conspicuously punctate-impressed upper surface. Neither surface depressions nor soralia are arranged in a reticulate pattern. It has a white medulla, a cyanobacterial photobiont, and prominent, large, white pseudocypbellae on the lower surface well delimited from the densely and evenly red-brown to brown-black tomentum. Thalli are dark grey-blue to blue-black when moist, olive brown to yellow-grey when dry. Apothecia very rare, generally absent. Spores fusiform-ellipsoid, apices pointed, yellow-brown, 1-septate (27.5–)30–32(–34) \times 6–7 μ m. It has a simple two-hopane chemistry.

P. haywardiorum is distinguished from *P. intricata* by the punctate-impressed upper surface and the \pm bullate lower surface with its prominent, large, raised pseudocypbellae, characters which also separate it from the isidiate species *P. argyrea*. It is separated from *P. dozyana* by the punctate-

impressed upper surface and the chemistry (*P. dozyana* is in the *P. crocata* group and has stictic acid metabolites and a hopane triol, and not just the two hopane-diols of *P. haywardiorum*).

DISTRIBUTION AND ECOLOGY. In the region known to date only from Norfolk Island where it is rare, occurring on *Araucaria heterophylla* and a tree fern stem (Elix et al., 1992). Known also from northern New Zealand and eastern Australia (Queensland and New South Wales).

15. *Pseudocyphellaria homalosticta* Vain. in *Philipp. J. Sci. Sect. C, Bot.* **8**: 117 (1913). Type: Phillipines. Luzon.

Prov. Rizal. Ad truncos arborum, February 1911, *M. Ramos*, Forest Bureau 13453 (TUR-VAINIO 10317-holotype).

Fig. 17.

Pseudocyphellaria amphistictoides Vain. in *Univ. Calif. Publ. Bot.* **12**: 6 (1924). Type: Tahiti. Fautaua Valley, May 1922, *W.A. Seitchell & H.E. Parks* 5443 (BM-isotype).

Thallus 3–10(–14) cm diam., irregularly spreading, loosely attached centrally, margins and apices ascending. *Lobes* (1–)2–6(–8) mm diam., subdichotomously to intricately branched. *Margins* entire at apices, soon becoming isidiate-

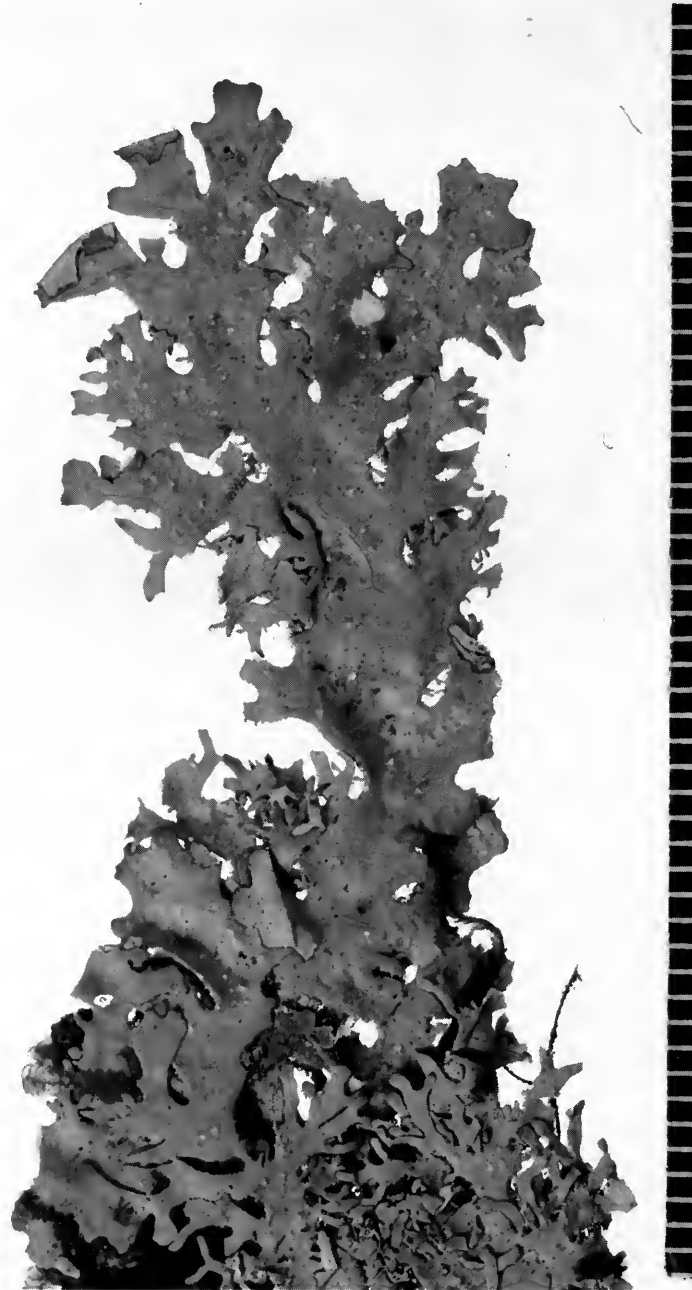


Fig. 17 *Pseudocyphellaria homalosticta*. Holotype (TUR-VAINIO 10317). Scale in mm.

phyllidiate or proliferating into long, narrow lobules, slightly thickened, ridged below, scattered white pseudocypHELLAE present, sometimes appearing \pm sorediate. *Upper surface* bright lettuce green when wet, pale olive green or buff brownish when dry, brittle, fragile, easily damaged when dry, pliable when wet, maculae and soredia absent. *Isidia* common, very variable, terete, simple at first becoming 1–3-branched to coralloid, 0.1 mm diam., to 5 mm long, becoming dorsiventral and phyllidiate, primarily marginal, rarely developing from margins of laminal pseudocypHELLAE. *Phyllidia* developing from terete isidia or intermixed and independent of them, dorsiventral, with minute pseudocypHELLAE below, elongate, to 5 mm long. *PseudocypHELLAE* white, scattered, punctiform, 0.1 mm diam. or less, \pm flat, occasionally with isidia developing from margins. *Medulla* white. *Photobiont* green. *Lower surface* pale whitish buff at margins, darkening centrally, occasionally \pm blackened at centre, glabrous, matt or glossy from margins to centre, or with scattered, thin tomentum centrally. *PseudocypHELLAE* white, prominent, widely scattered, conical-verruciform, rounded, 0.1–0.3 mm diam., margins not prominent.

Pycnidia solitary, \pm marginal, hemispherical, 0.1 mm diam. or less, ostiole punctate, dark red-brown.

Apothecia rare, marginal, rounded, 0.5–1.5 mm diam., subconvex to plane, sessile, constricted at base, exciple minutely corrugate-scabrid, persisting as verrucose margin to disc, pale buff or pinkish, translucent when wet, disc pale to dark red-brown, smooth, epruinose. *Epithecium* pale yellow-brown, 8–12 μ m thick. *Hymenium* colourless, 70–85 μ m tall. *Ascospores* pale yellow-brown, 1-septate, fusiform-ellipsoid, apices rounded or pointed, 25–28 \times 6.5–8 μ m.

CHEMISTRY. Methyl gyrophorate (tr.), \pm gyrophoric and congyrophoric acids, 7 β -acetoxyhopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *PseudocypHELLARIA homalosticta* has a white medulla, a green photobiont and white pseudocypHELLAE on both upper and lower surfaces and characteristically at the margins of lobes where they can sometimes appear \pm sorediate. It has marginal and occasionally laminal terete isidia which may become dorsiventral flattened phyllidia. It has a basic two-hopane chemistry, with or without accessory depsides. It is distinguished from *P. prolificans* which has marginal and laminal phyllidia and lobules, and a punctate-impressed upper surface which is without pseudocypHELLAE; from *P. multifida* which has a smooth upper surface without pseudocypHELLAE and simple to squamiform phyllidia; and from *P. reineckeana* which has entire margins without phyllidia or isidia.

DISTRIBUTION AND ECOLOGY. A species endemic to the south-west Pacific where it occurs from Fiji eastwards to the Marquesas Islands (Fig. 18). It is an epiphyte of trees and shrubs in dense, montane rainforest, 900–1200 m.

SPECIMENS EXAMINED. **Fiji:** Viti Levu, Nandarivatu, *Asplund* s.n. (BM, Herb. L. Arvidsson); *Degener* 31811 (Herb. Aptroot); Mt Nanggaranambuluta [Lomalangi], *Smith* 4818 (BM, L); *Smith* 4833 (BM); ridge between Mt Nanggaranambuluta and Mt Namama east of Nandarivatu, *Smith* 5009 (L); Mt Victoria, *Lam* 6824 (L); *Green* (BM). **Ovalu.** Sine loco, *Gräffe* (W). **Rarotonga:** Tiriora, *Parks* 22395 (COLO); sine loco, *Parks & Parks* 22363a (COLO). **Marquesas Is:** Ua Pu, *Jones* 1178 (Herb. Aptroot). **Nuku Hiva.** Tovii, *Peake* (BM).

16. *PseudocypHELLARIA intricata* (Delise) Vain. in *Hedwigia* 37: 35 (1898). *Sticta intricata* Delise in *Mém. Soc. linn. Normandie* 2: 96 pl. 7 fig. 33 (1825). *Stictina intricata* (Delise) Nyl., *Syn. meth. lich.* 1(2): 334 (1860). *Cyanisticta intricata* (Delise) Gyeln. in *Lilloa* 3: 76 (1938). Type: Ile de Bourbon [Réunion], *Bory de St-Vincent* (PC-

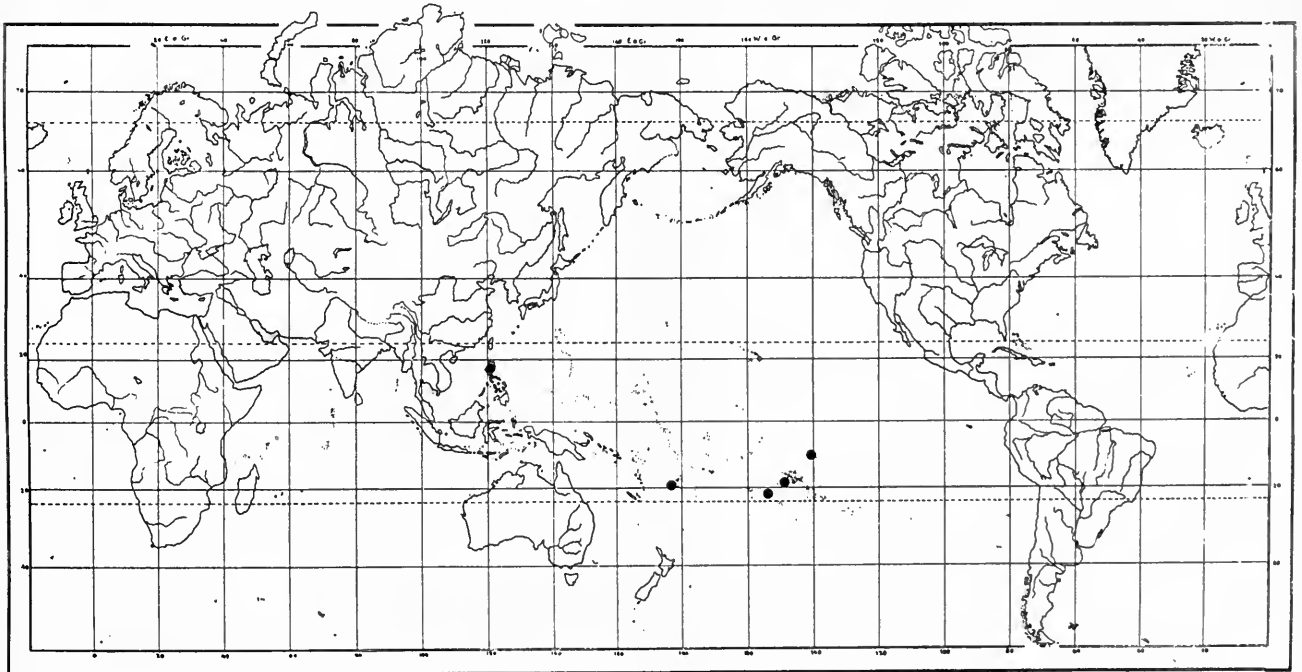


Fig. 18 Distribution of *PseudocypHELLARIA homalosticta*.

LENORMAND-lectotype (Galloway & James, 1986: 437 (1986)). For additional synonymy see Galloway & James (1986: 437) and Galloway (1988: 169).

Sticta dolera Hue in *Nouv. Archs Mus. Hist. Nat. Paris* IV, 3: 98 (1901). Type: [Réunion] Ins. Bourbon, sine loco, *Lepervanche-Mezières* (PC-HUE 769-lectotype, selected here).

Cyanisticta philippinica Gyeln. in *Reprim Spec. nov. Regni veg.* 29: 298 (1931). Type: Philippines, Luzon, Prov. Benguet, Pauai, 2100 m, *R.C. McGregor* (D-not seen).

Pseudocyphellaria intricata is a widespread cosmopolitan species having a wide range of variation and paralleling the diversity of morphology seen in *P. crocata*. For a detailed description of the species see Galloway (1988: 169–174).

CHEMISTRY. Tenuiorin (tr.), methyl gyrophorate (tr.), 7 β -acetoxypopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *Pseudocyphellaria intricata* is dark slate-blue to blue black when wet, pale greyish to buff when dry; it has irregularly lacinate to somewhat rounded lobes, with sinuous, incised or \pm entire, generally sorediate margins. It has a white medulla, a cyanobacterial photobiont, a pale buff to brown, tomentose lower surface with occasional, scattered, white pseudocyphellae and a \pm shining upper surface which may have scattered, erose, white to brownish laminal soralia. It has a characteristic, basic two-hopane chemistry (Galloway, 1988; Wilkins, 1993). It is distinguished from *P. haywardiorum* by its smooth upper surface and its lower surface which is not bullate; from *P. argyracea* which has terete isidia associated with the laminal pseudocyphellae; and from *P. dozyana* which has a faveolate upper surface and hopane-6 α , 7 β , 22-triol as a major metabolite.

DISTRIBUTION AND ECOLOGY. Widespread throughout the

tropics and also in cool temperate regions of the world (Galloway, 1988, 1992; Galloway & Arvidsson, 1990). In the palaeotropics (Fig. 19) it occurs in humid, shaded woodland and montane forest and cloud forest from 400 to 2000 m (to 3600 m in New Guinea). It is nowhere a common species.

SPECIMENS EXAMINED. **Africa. Kenya:** Mt Kenya east side, Themwe, *Swinscow* (BM); 2 km west of Irangi Forest Station, *Swinscow* (BM). **South Africa:** Smith's Peak, *Leighton* 942 (L); Knysna, *Almborn* [Lichenes africana 10] (L); *Werdermann* & *Oberdieck* 920 (B); Table Mountain, *Sipman* 20.189 (B); 7–800 m, [on soil] *Werdermann* & *Oberdieck* 49, 51 (B); between Devils Peak and Table Mountain, *Wilms* (B). **Madagascar:** Amboluimiloimbo Forest, *Forsyth Major* 543 (BM). **Réunion:** Piton de la Grand Montée, près des sources Reihlac, *de Sloover* 17.258 (LG). **Sri Lanka:** Horton Plains, World's End, *Bohlin* (S). **Malaysia: Pahang.** Fraser's Hill, *Burkill* 2073 (L); *Dransfield* 514 (BM); Cameron Highlands, *Bowen* 4090 (E). Sabah. Mt Kinabalu, *Samsudin* (UKMB). **Indonesia. Java:** Herb. Lugd. Batav. (L); Mt Ardjuno, *Groenhart* 1855, 1982 (L); Mt Panderman, *Groenhart* 1954 (L); Mt Lawu, *Clason* 985 (L); Mt Gede, *van Ootstroom* 145900 (L). **Philippines: Luzon.** Benguet, *Merrill* 7952 (BM); Mt Santo Tomas, *Aptroot* 20454, 20450, 20451 (Herb. Aptroot); *Sipman* 21812 (B). **Papua New Guinea: Morobe.** Saruwaged Range, *Sipman* 24330, 24337, 24387 (B); Kaisinik, *Kashiwadani* 10743 (TNS); Wau, Mt Kaindi, *Kashiwadani* 10588, 10593 (TNS); *Streimann* 34024 (CBG); near Honzeukngon village, *Aptroot* 17931–2, 18025 (Herb. Aptroot); Gumi Divide, *Streimann* 22760, 22769 (CBG); Koke Village, *Streimann* & *Tamba* 11730 (CBG); Manki Trig, *Streimann* & *Bellamy* 12969 (CBG). **Eastern Highlands.** Wopeia, *Streimann* 18328a (B); Chimbu. Pindaunde Valley, *Aptroot* 32740 (Herb. Aptroot); *Weber* & *McVean* (COLO); Lake Piunde, *Sipman* 22121 (B); Mt Wilhelm, *Kashiwadani* 10846, 10885, 10998, 11199, 11417 (TNS); *Aptroot* 18243

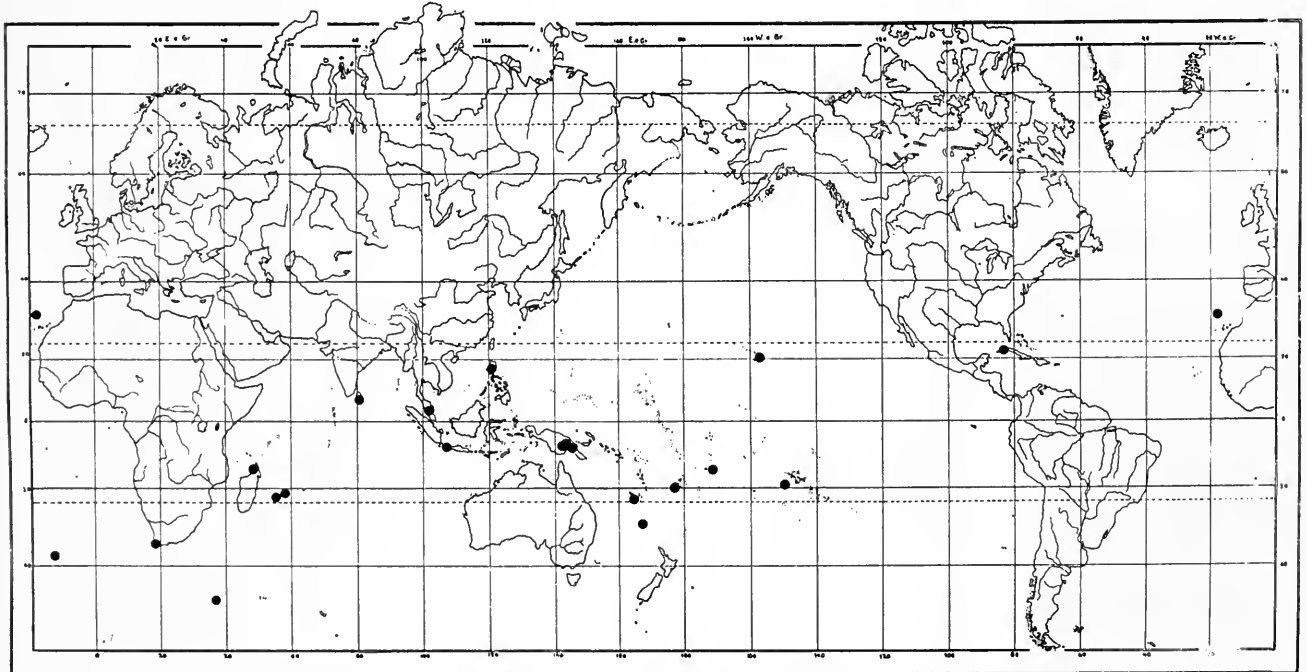


Fig. 19 Distribution of *Pseudocyphellaria intricata* in the palaeotropics.

(Herb. Aptroot); *McVean* 66115 (CBG); Imbuka Ridge above Lake Aunde, *Weber & McVean* (COLO); Yagle Village, *Kawagle* 2 (CBG); Goroka, Daulo Pass, *Aptroot* 31660 (Herb. Aptroot); Mt Gahavisuki Nature Reserve, *Aptroot* 18802, 18842 (Herb. Aptroot); 1500 m, *Streimann & Kairo* 18155 (CBG). **Madang**, Finisterre Range. Teptep Village, *Aptroot* 31931, 32288, 32295 (Herb. Aptroot). **Central**. 2 km N. of Waiotape Airstrip, *Kashiwadani* 11559, 11653, 12244 (TNS); Mt Albert-Edward, *Kashiwadani* 11776 (TNS); Varirata National Park, *Streimann & Vinas* 14472 (CBG). **Southern Highlands**. Iaro River, *Streimann* 23823 (CBG). **Western Highlands**. Kagamuga, *Streimann* 21712 (CBG). **Enga**. Mape Creek, *Streimann* 21569, 22112 (CBG). **New Caledonia**: Tinchialit Camp, *Cheeseman* (BM); sine loco, *Compton* (BM). **Norfolk Island**: Mt Pitt Reserve, Mt Bates, *Streimann* 34386, 34331 (CBG). **Fiji**: sine loco, *Wilson* (MEL). **Samoa**: **Upolu**. *Schultz-Motel* 3496 (B). **Tahiti**: sine loco, *Jelinek* 53 (W). **Hawaiian Islands**: **Oahu**. Koolau Mountains, ridge from Tantalus to Puu Konahuanui, *Smith* 130as (Herb. Smith).

17. *Pseudocypbellaria maculata* D.J. Galloway in *Bull. Br. Mus. nat. Hist. (Bot.)* 17: 187 (1988). Type: New Zealand. South Island, Nelson, Maruia River, Speargrass Flat, near Springs Junction, on twigs of wayside shrubs, 22 September 1981, *D.J. Galloway* (CHR 381022-holotype; BM-isotype).

Pseudocypbellaria maculata is a member of the *P. crocata* complex of taxa characterized by a white medulla, a cyanobacterial photobiont and yellow pseudocypbellae on the lower surface. The species is described in detail in Galloway (1988: 187–191) and material examined from New Guinea agrees in all respects with New Zealand collections from which the species was described.

CHEMISTRY. Methyl evernate (tr.), tenuiorin, methyl lecanorate (tr.), methyl gyrophorate, evernic acid (tr.), gyrophoric acid (tr.), hopane-6 α , 7 β , 22-triol, norstictic (tr.), salazinic, consalazinic, galbinic acids, pulvinic dilactone, pulvinic acid and calycin.

OBSERVATIONS. *Pseudocypbellaria maculata* is dark slate-blue to brown black, suffused red-brown when wet, olivaceous-grey to red-brown when dry; it has a white medulla, a cyanobacterial photobiont, a conspicuously faveolate upper surface with a well-defined reticulate pattern of white (photobiont-free) maculae best seen when the thallus is wet ($\times 10$ lens), and yellow pseudocypbellae on the lower surface and visible at the lobe margins. It lacks isidia, soredia, phyllidia, pseudocypbellae or tomentum on the upper surface. Its loose, straggling habit (especially in alpine grassland habitats where it is often best-developed) is also characteristic. It is rarely fertile. *P. maculata* is distinguished from *P. gilva* by its thinner more fragile and papery thallus, by its markedly faveolate upper surface with characteristic sharp, reticulate ridges, and the pale to buff silkily white-tomentose lower surface; from *P. crocata* by the absence of soredia; from *P. crocatoides* by the lack of marginal proliferations; from *P. desfontainii* by the absence of isidia; and from *P. neglecta* by the absence of phyllidia.

DISTRIBUTION AND ECOLOGY. An epiphyte of trees and shrubs in montane rainforest and high alpine grassland habitats of high humidity in New Guinea, 1200–3810 m. Also in

New Zealand where it occurs in rainforest and alpine grassland habitats (Galloway, 1988).

SPECIMENS EXAMINED. **Irian Jaya**: Carstenz Mountains, *Hope* (COLO). **Papua New Guinea**: **Eastern Highlands**. Chimbu, Pindaunde Valley, *Stone* 9903 (Herb. Aptroot); *Weber & McVean* (Herb. Aptroot); *Aptroot* 32732 (Herb. Aptroot); Mt Wilhelm, *Kashiwadani* 11000, 11087, 11128, 11335, 11354 (TNS); *McVean* 66179 (CBG); Goroka, Daulo Pass, *Streimann & Kairo* 18138 (CBG); Mt Gahavisuki Nature Reserve, *Aptroot* 18803 (Herb. Aptroot). **Morobe**. Mt Sarawaket [Saruwaged] Southern Range, *Koponen* 32164, 32640 (Herb. Aptroot); track to Mt Missim, *Bellamy* 211 (CBG); Wau, Mt Kaindi, *Kashiwadani* 10537 (TNS); Mt Missim, *Kashiwadani* 10412 (TNS); Slate Creek and Gumi Creek Divide, *Streimann* 13978 (CBG); Araulu Logging Area, *Streimann* 13619 (CBG). **Central**. 2 km N. of Waiotape Airstrip, *Kashiwadani* 12257 (TNS). **Southern Highlands**. Margarima-Tari Road, *Streimann* 24380 (CBG). **Western Highlands**. Yobobos, *Hoogland & Schodde* 7640 (COLO). **Enga**. Mape Creek, *Streimann* 21540 (CBG).

18. *Pseudocypbellaria multifida* (Nyl.) D.J. Galloway & P. James in *Lichenologist* 12: 301 (1980). *Sticta multifida* Nyl., *Syn. meth. lich.* 1(2): 363 (1860). *Sticta dissecta* Laurer in *Linnaea* 2: 41 (1827), non *S. dissecta* (Sw.) Ach. (*Meth. Lich.*: 279 (1803)). *Crocodia multifida* (Nyl.) Trevis., *Lichenotheca veneta* exs. 75 (1869). *Lobaria multifida* (Nyl.) Hellb. in *Bih. K. svenska VetenskAkad. Handl.* 21(2/13): 38 (1896). Type: Nov. Holland [Australia], *Sieber* 45 (BM-lectotype (Galloway, 1988: 199)). For additional synonymy see Galloway (1988: 199–200).

Pseudocypbellaria multifida is a palaeotropical taxon with a highly plastic morphology and having a white medulla and pseudocypbellae, a green algal photobiont and a basic two-hopane chemistry. It is discussed in detail in Galloway (1988: 199–204).

CHEMISTRY. 7 β -acetoxyhopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *Pseudocypbellaria multifida* is bright lettuce-green when wet, pale greenish grey to buff brownish when dry; it has very variable, rather delicate lobes ranging from \pm broadly rounded to more usually narrow and highly divided, entangled-imbricate, the margins ragged-incised to lobulate or richly phyllidiate. The upper surface is smooth, undulate or shallowly wrinkled, punctate-impressed, with occasional, white maculae towards margins, and occasionally to densely developed, simple, squamiform, palmate-coralloid to \pm strap-like phyllidia. It has a white medulla, a green photobiont, and a pale whitish, glabrous, glossy, smooth or shallowly wrinkled lower surface, with a usually poorly developed, thin, short, velvety tomentum centrally, and with scattered, white, fleck-like pseudocypbellae most noticeable at margins. Apothecia are rare. It has a basic two-hopane chemistry. It is distinguished from *P. prolificans* by its plane or undulate, not distinctively punctate-impressed upper surface, by the unthickened, \pm naked margins of the lower surface and by the frequently \pm squamiform phyllidia; from *P. insculpta* which has a cyanobacterial photobiont and a punctate-impressed upper surface; and from *P. homalosticta* which has pseudocypbellae on the upper surface which occasionally become \pm sorediate.

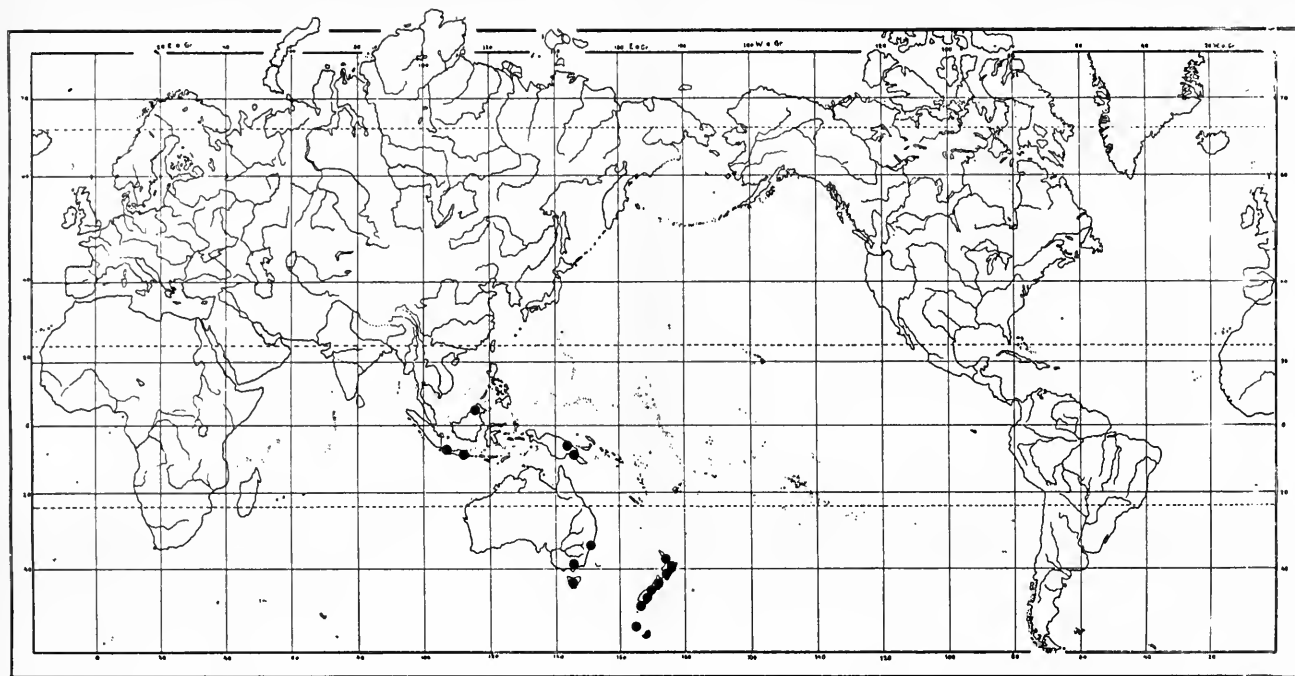


Fig. 20 Distribution of *Pseudocyphellaria multifida* in the palaeotropics.

DISTRIBUTION AND ECOLOGY. From Sabah and Java eastwards to New Guinea (Fig. 20) and southwards to Australasia where it is common throughout New Zealand (Galloway, 1988) and in Tasmania (Kantvilas, 1988). In the palaeotropics it is an epiphyte of trees and shrubs and overgrows rotting logs in humid montane rainforest, 1000–2900 m.

SPECIMENS EXAMINED. **Malaysia: Sabah.** Mt Kinabalu, *Samsudin* (UKMB). **Indonesia. Java:** East Java. Mt Tengger, *Groenhart* 260, 1835, 7265 (L); Mt Kawi, *Groenhart* 7248, 7249, 7256, 7257, 7258 (L); Mt Ardjuno, *Groenhart* 1534, 1867, 6254 (L); Mt Andjasmoro, *Groenhart* 1817, 1874, 1875, 7230 (L); West Java. Tjibodas, Mt Gede, *van Ootstroom* 14207 (L); *ibid.*, *Groenhart* 1801 (L); Batavia. Mt Pantjar, *Schiffner* 2978 (WU); Preanger, Tjibodas *Schiffner* (WU). **Papua New Guinea: Morobe.** Mt Kaindi, *Streimann & Bellamy* 17670 (CBG); Kauwara River, *Kairo* 671 (CBG); Koke Village, *Streimann & Tamba* 11665 (CBG); Kaurau, *Kairo* 379 (CBG); Spreader Divide, *Streimann & Tamba* 11951 (CBG); Honzeukngon village, *Aptroot* 17861 (Herb. Aptroot). **Eastern Highlands.** Chimbu. Mt Wilhelm, *Kashiwadani* 11190 (TNS); Goroka. Mt Gahavisuki Nature Reserve, *Aptroot* 18778, 18804, 18829 (Herb. Aptroot). **Southern Highlands.** Onim Forestry Station, *Streimann* 24667 (CBG). **Enga.** Mape Creek, *Streimann* 22084 (CBG).

19. *Pseudocyphellaria neglecta* (Müll. Arg.) H. Magn. in *Acta Horti gothoburg.* **14:** 30 (1940). *Stictina neglecta* Müll. Arg. in *Flora, Jena* **70:** 58 (1887). Type: Australia, New England, sine collectoribus nomine (G002121-holotype). For additional synonymy see Galloway (1988: 207; 1992: 183).

Pseudocyphellaria neglecta is a characteristic phyllidiolate species in the *P. crocata* complex and is discussed in detail in Galloway (1988: 207–210).

CHEMISTRY. Calycin, pulvinic dilactone (tr.), pulvinic acid, tenuiorin, methyl gyrophorate, stictic, constictic, norstictic (tr.), cryptostictic (tr.), salazinic (tr.) acids, 6 α -acetoxyhopane-7 β , 22-diol (minor), 7 β -acetoxyhopane-6 α , 22-diol (tr.), hopane-6 α , 7 β , 22-triol (major), hopane-7 β , 22-diol (minor), hopane-15 α , 22-diol (tr.), 7 β -acetoxyhopane-22-ol (tr.), 15 α -acetoxyhopane-22-ol (tr.), retigeranic acid (minor) and traces of unidentified triterpenoids.

OBSERVATIONS. *Pseudocyphellaria neglecta* is lead-grey to dark blue-black or suffused red-brown when wet, olivaceous-brown, red-brown, brownish yellow or reddish to \pm blackened in exposed habitats when dry; it has linear-elongate to broadly rounded lobes with entire to crenate-incised to densely phyllidiolate margins. The upper surface is undulate, wrinkled to subfaveolate, occasionally with squamiform phyllidia regenerating from cracks or scattered over upper surface, often eroding apically and appearing sorediate, or breaking off and leaving small yellow scars like pseudocyphellae. It has a white medulla, a cyanobacterial photobiont and yellow pseudocyphellae on the lower surface. It has a complex chemistry containing pigments, depsides, depsidones and hopane-6 α , 7 β , 22-triol as the major triterpenoid. For differences between *P. crocata*, *P. crocatoides*, *P. gilva* and *P. dozyana* see above under these taxa.

DISTRIBUTION AND ECOLOGY. Widespread in the South Pacific from Mt Kinabalu (Sipman, 1993) eastwards to New Guinea and Tahiti (Fig. 21). It is also known from Australia (where it is extremely common and the most widely collected species), New Zealand (Galloway, 1988) and Chile (Galloway, 1992) where it tends to favour rather dry sites with high light intensities. In the palaeotropics it is found in more humid situations; on roadside banks, on rocks, stumps, fallen branches and rotting logs on the forest floor and as an

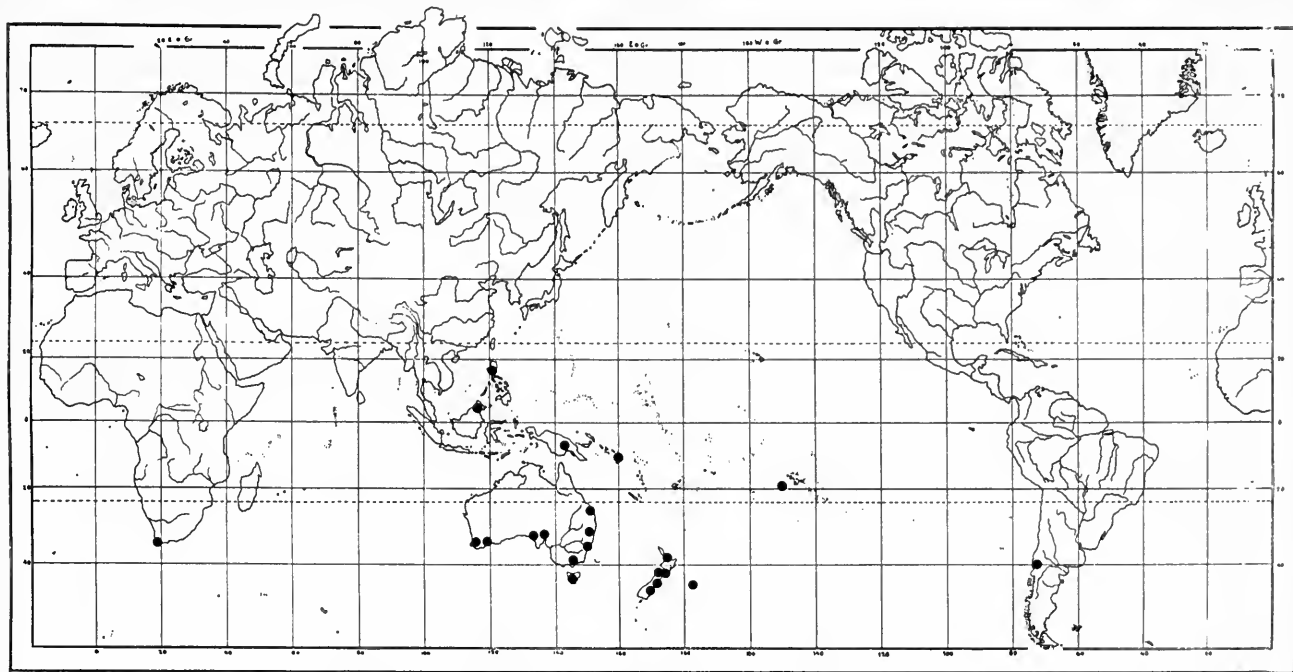


Fig. 21 Distribution of *Pseudocyphellaria neglecta* in the palaeotropics.

epiphyte of trees and shrubs in montane forest and mossy cloudforest, 700–3500 m.

SPECIMENS EXAMINED. **Malaysia:** Sabah. Mt Kinabalu, *Sipman & Tan* 30961 (B); *Samsudin* (UKMB). **Indonesia:** Sumatra. Mt Horintji, *Meyer* 7791 (L). **Philippines:** Luzon. Benguet. Mt Santo Tomas, *Sipman* 21750 (B). **Papua New Guinea:** Central. Mt Victoria area, Iswan Swamp, *van Royen* 10957 (Herb. Aptroot). **Madang.** Finisterre Range, Teptep Village, *Aptroot* 30955 (Herb. Aptroot). **Morobe.** Mt Kaindi, *Weber & McVean* (Herb. Aptroot, COLO); *Streimann* 19908, 33171, 34072, 34078 (CBG); Herzog Mountains, *Streimann & Umba* 11130 (CBG); Near Honzeukngon village, *Aptroot* 18019 (Herb. Aptroot); Gumi Divide, *Streimann* 25731 (CBG); Aiuwa-Bakia Track, *Streimann & Tamba* 12347 (CBG); Eraulu Logging Area, *Kairo* 338 (CBG); Mt Missim Track, *Streimann* 22923 (CBG). **Eastern Highlands.** Goroka. Daulo Pass, *Weber & McVean* (COLO); Mt Gahavisuki Nature Reserve, *Aptroot* 18806 (Herb. Aptroot); Chimbu. Mt Wilhelm area, *Aptroot* 18321, 18407, 18601, 18654 (Herb. Aptroot). **Southern Highlands.** Onim Forestry station, *Streimann* 24559 (CBG). **Enga.** Mape Creek, *Streimann* 21535, 21554 (CBG). **Solomon Islands:** Guadalcanal Island. Mt Popomansiu, *Hill* 9558 (BM). **Tahiti:** Aorai, *v. Balgooy* 1864a (Herb. Aptroot).

20. *Pseudocyphellaria pickeringii* (Tuck.) D.J. Galloway in *Bull. Br. Mus. nat. Hist. (Bot.)* 17: 218 (1988). *Sticta pickeringii* Tuck., *U.S. Expl. Exped.* 17 (Bot.): 138 (1874). Type: New Zealand, Bay of Islands, Wilkes Expedition, sine collectoribus nomine (FH-holotype).

Pseudocyphellaria flavicans auct., non (Hook.f. & Taylor) Vain. For additional synonymy see Galloway (1988: 218–219).

Pseudocyphellaria pickeringii is a characteristic yellow-

medulla, isidiate, widespread palaeotropical lichen which is discussed in detail in Galloway (1988: 218–224).

CHEMISTRY. Pulvinic acid, pulvinic dilactone, calycin, 2 α , 3 β , 22 α -triacetoxystictane, 2 α , 3 β -diacetoxystictane-22-ol, stictane-3 β -22 α -diol, 2 α -acetoxystictane-3 β , 22 α -diol, 3 β -acetoxystictane-2 α , 22 α -diol, stictane-2 α , 3 β , 22 α -triol, 3 β , 22 α -diacetoxystictane, 2 α , 3 β -diacetoxystictane-22-ol, 3 β -acetoxystictane-22-ol, pseudocyphellarin A, isopseudocyphellarin A, nephroarctin, phenarctin, 2'-O-methylphenarctin, 1'-chlorophenarctin, 2'-O-methylisopseudocyphellarin A, 2'-O-methylpseudocyphellarin A (Elix et al., 1992).

OBSERVATIONS. *Pseudocyphellaria pickeringii* is bright lettuce-green suffused golden-yellow when wet, pale lemon-yellow to golden yellow when dry; it is a palaeotropical species forming irregular rosettes on bark, rocks and soil. It has variable, \pm rounded to complexly divided, rather ragged, incised lobes whose margins are \pm isidiate-phyllidiate. The upper surface is coriaceous, smooth to faveolate in parts to \pm scabrid-areolate ($\times 10$ lens), with marginal and laminal terete isidia and flattened, \pm dorsiventral phyllidia present. It has a yellow medulla, a green photobiont, and the lower surface is pale yellow to red-brown with a velvety pale tomentum and scattered, yellow, often inapparent pseudocyphellae. Apothecia are sparse or absent, though occasionally frequent in some specimens, sessile to subpedicellate with a conspicuous, whitish buff, coarsely verrucose-scabrid exciple. Spores are colourless, 1–3(–5)-septate, fusiform-ellipsoid, 25–29.5(–32) \times 6.5–7 μ m. It has a complex chemistry of pigments and stictane triterpenoids (Elix et al., 1992; Wilkins, 1993). It is distinct from *P. aurata* which has characteristic marginal, labriform yellow soralia; from *P. clathrata* which has entire margins without either isidia, phyllidia or soredia; and from *P. poculifera* which has fragile, marginal sorediate isidia.

DISTRIBUTION AND ECOLOGY. Widespread in the palaeotro-

pics from the Philippines eastwards to Hawaii and the Marquesas (Fig. 22) and common in the South Pacific in New Zealand (Galloway, 1988) and Australia. On living and dead branches of trees and shrubs (often in canopy branches) in humid montane rainforest and in open habitats of high light, 200–2700 m.

SPECIMENS EXAMINED. **Philippines:** Luzon, Benguet, Baguio, Williams 1636 (B); Merrill 7953, 7956 (BM); Ramos 13510 (BM); Mt Santo Tomas, Degelius as-822 (UPS). **Papua New Guinea:** Morobe, Saruwaged Range, Sipman 24428 (B); Yimimba, Streimann 19025 (CBG); Mt Kaindi, Kashiwadani 10524, 10567 (TNS); near Honzeukngon village, Aptroot 18021 (Herb. Aptroot); Gumi Divide, Streimann 22771 (CBG). **Madang.** Finisterre Range, Teptep Village, Aptroot 31938, 32007, 32021, 32293 (Herb. Aptroot). **Eastern Highlands.** Goroka, Daulo Pass, Streimann 18020 (CBG); Mt Gahavisuki, Lambley 100/84, 102/84 (BM); Kassar Pass, Streimann & Umba 11476 (CBG). **Central.** Mt Albert-Edward, Kashiwadani 11793 (TNS); Myola, Lambley 92/85 (BM). **Western Highlands.** Baiyer-Jimi Divide, McVean 68181 (CBG). **New Caledonia:** Sarramea, Col d'Amieu, Hill 11959, 11982 (BM); sine loco, Compton 1300 (BM). **Norfolk Island:** Mt Pitt Reserve, Streimann 31931, 31944 (CBG); track from Mt Bates, Streimann 34252 (CBG); Selwyn Pine Road, Hoogland 6587 (L). **Samoa:** Tutuila, Lutisa? (B). **Hawaiian Islands:** Oahu, Pauoa, Heller (BM, L, US); Waianae Mountains, Mokuleia Forest Reserve, Smith 3151 (Herb. Smith); Koolau Mountains, Kahuku Forest Reserve, Smith 1660 (Herb. Smith); Honolulu, Faurie 441 (BM). **Kauai.** Hanapepe Valley, Heller (BM, L); Faurie 87 (BM). **Maui.** South slope of Haleakala, Auwahi, James & Smith 84/2 (BM); Haleakala, Faurie 591, 592 (BM). **Marquesas Islands:** Nukuhiva, Tovii, Peake (BM).

21. *Pseudocyphellaria poculifera* (Müll. Arg.) D.J. Galloway

& P. James in *Lichenologist* 12: 301 (1980). *Sticta poculifera* Müll. Arg. in *Flora, Jena* 65: 304 (1882). Type: Lord Howe Island, Mt Gower, F. v. Mueller (G 002123-holotype; BM, MEL-isotypes).

This characteristic rosette-forming to irregularly spreading, yellow-medulla species is described in detail in Galloway (1988: 224–228) and in Elix et al. (1992: 71–72).

CHEMISTRY. Pulvinic acid, pulvinic dilactone, calycin, 3 β -acetoxyfern-9(11)-en-12-one, fern-9(11)en-3 β , 12 β -ol, 3 β -hydroxyfern-9(11)-en-12-one, 3 β -acetoxyfern-9(11)-en-12 β -ol, 3 β -acetoxyfern-9(11)-en-19 β -ol and unidentified triterpenoids (Elix et al., 1992).

OBSERVATIONS. *Pseudocyphellaria poculifera* is bright lettuce-green suffused yellow-gold when wet, pale green-grey when dry; it is a palaeotropical species characterized by a yellow medulla, a green photobiont, yellow pseudocyphellae on the lower surface, greenish yellow, mainly marginal (occasionally also laminal), densely clustered, minutely coralloid, rather delicate isidia which are \pm corticate at first, but soon erode and become sorediate. It is quite commonly fertile, the apothecia being marginal or submarginal and distinctly pedicellate and with granular isidiate margins. Spores are pale to dark red-brown, 3-septate, broadly fusiform-ellipsoid, (18–)20–23(–25) \times 5.5–7.5 μ m. It has a complex chemistry of pigments and fernene triterpenoids (Elix et al., 1992). It is readily distinguished from the related *P. aurata* which has characteristic linear-labrifiform marginal soralia; and from *P. pickeringii* in the nature of the isidia, the structure of the exciple, the attachment of the apothecia, and in the size and colour of the spores.

DISTRIBUTION AND ECOLOGY. A palaeotropical species (Fig. 23) which is known from East Africa (where it is extremely rare) and from Peninsular Malaysia and the Philippines

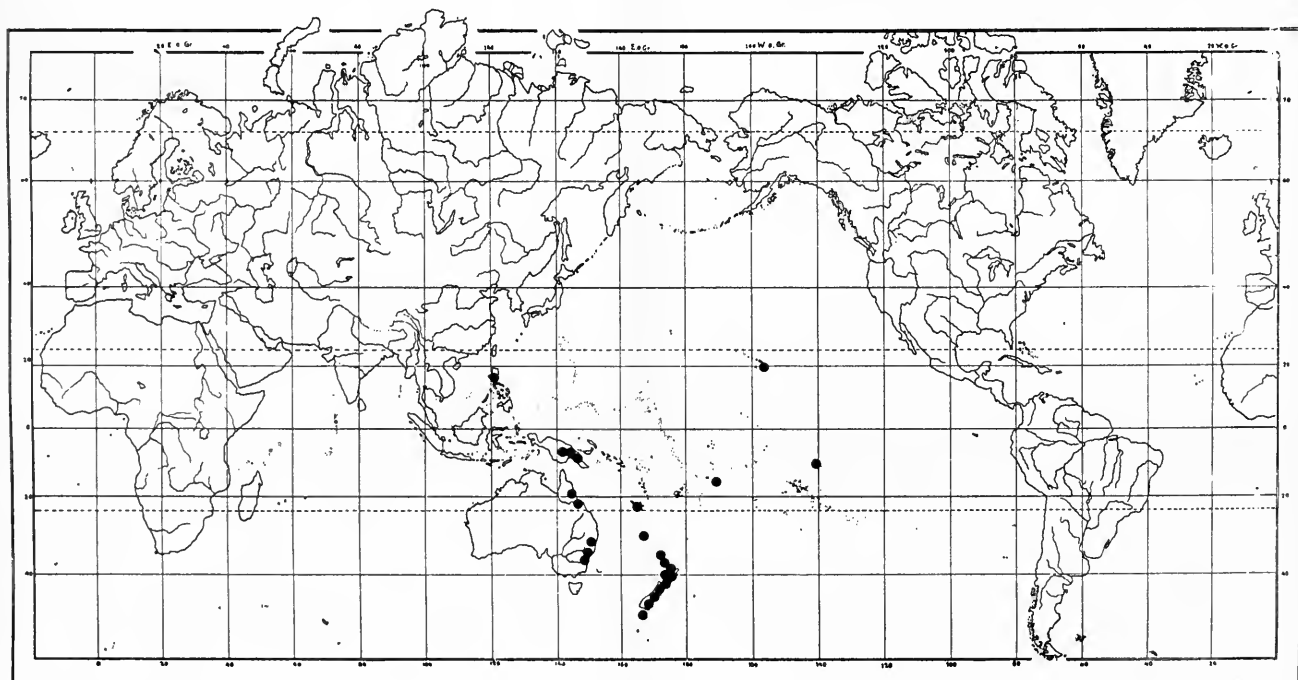


Fig. 22 Distribution of *Pseudocyphellaria pickeringii* in the palaeotropics.

eastwards to Fiji and Norfolk Island where it is common (Elix et al., 1992) and southwards to eastern Australia and northern New Zealand (Galloway, 1988). It occurs on bark and twigs of a variety of phorophytes in open conditions, occasionally on rocks also. It has an altitudinal range from sea level to 750 m throughout most of its range; the sole East African specimen seen was from 2100 m.

SPECIMENS EXAMINED. **Africa.** **Uganda:** Butandiga Bugishu, A.S.T. 2555 (BM). **Malaysia:** **Pahang.** Fraser's Hill, Galloway (KEP). **Indonesia.** **Java:** Near Wonosobo, Oka 4087 (L). **Papua New Guinea:** **Morobe.** Kasu Village, Kairo 563, 573 (CBG). **New Caledonia:** **Sarramea.** Col d'Amieu, Hill 11872, 11883 (BM). **Norfolk Island:** Cascade, Ralston (BM, COLO); Prince Phillip Drive, Streimann 36480 (CBG); Capt. Cook Monument, Streimann 32045 (CBG); Mt Pitt Reserve, track to Hollow Pine, Streimann 31994 (CBG); Mt Pitt Road, Streimann 31943, 31923 (CBG); King Fern Valley, Streimann 34552 (CBG); Mt Pitt, Streimann 34814 (CBG); track at end of Sellwyn Pine Road, Streimann 34648, 34655 (CBG); off Selwyn Pine Road, Filmy Fern Trail, Streimann 32106, 32086, 32159 (CBG); Mt Bates, Streimann 34228 (CBG); Bird Rock Track, Streimann 34899 (CBG); track from Mt Bates, Streimann 34300 (CBG); summit of Mt Bates, Ralston 90b (BM); east side Mt Bates, Hoogland 11.157 (BM); north side Mt Bates, Green 1424 (BM); Now-now Valley, Hoogland 11.257 (BM); 'High ground', sine loco, Milne (BM). **Fiji:** **Viti Levu.** Nandarivatu, Smith 5965 (L); sine loco, Milne (BM).

22. ***Pseudocyphellaria prolificans*** (Nyl.) Vain. in *Philipp. J. Sci. sect. C, Bot.* **8:** 117 (1913). *Sticta prolificans* Nyl. in *Annls Sci. Nat. Bot.* **IV, 15:** 42 (1861). *Crocodia prolificans* (Nyl.) Trevis., *Lichenotheca veneta* exs. 75 (1869). Type: New Caledonia, ad cortices sylvarum in Kanala, Vieillard 1795 (PC-holotype).

Fig. 24.

Pseudocyphellaria multipartita Vain. in *Philipp. J. Sci. Sect. C, Bot.* **8:** 116 (1913). Type: Philippines, Luzon, Batangas Prov. Ad truncos arborum et supra muscos, November 1907, H.M. Curran & M.L. Merritt Forest Bureau 7809 (TUR-VAINO 10291-lectotype, selected here).

Thallus very variable, orbicular to irregularly spreading, often forming densely entangled clones, 5–12(–18) cm diam., loosely to closely attached centrally, margins and apices free, \pm ascending. **Lobes** very variable, most commonly rather narrow, linear-laciniate, rather ragged, (1–)2–5(–8) mm wide, 1–4(–8) cm long, to occasionally broadly rounded, 8–15 mm wide, subdichotomously branching at or near apices, complex-imbricate, entangled centrally, apices truncate, rounded or \pm furcate, divergent. **Margins** entire towards apices becoming densely phyllidiate towards centre, noticeably thickened above and below, pseudocyphellae often prominent on lower margin. **Upper surface** lettuce-green to olive-green when wet, undulate, irregularly to markedly dimpled, punctate-impressed, often with dense to widely scattered papillae (use $\times 10$ lens), thin and papery to tough, coriaceous, without isidia, maculae, pseudocyphellae or soredia. **Phyllidia** common, conspicuous, mainly marginal but also laminal, occasionally terete at first, soon becoming flattened-dorsiventral, constricted at base, 0.1–0.5 mm wide, 1–5(–10) mm tall, simple, branched to \pm coralloid, single or densely clustered and proliferating. **Medulla** white. **Photobiont** green. **Lower surface** whitish or pale yellow-brown or pinkish fawn, smooth or wrinkled, glossy at margins to chestnut or red-brown centrally, or uniformly pale from margins to centre, tomentose from margins to centre or only in older parts, tomentum very variable, thick and woolly to thin, ragged and scattered in patches, white, silky, to dark-brown, red-brown or \pm blackened. **Pseudocyphellae** common, conspicuous, white, round to irregular, 0.1–1.5 mm

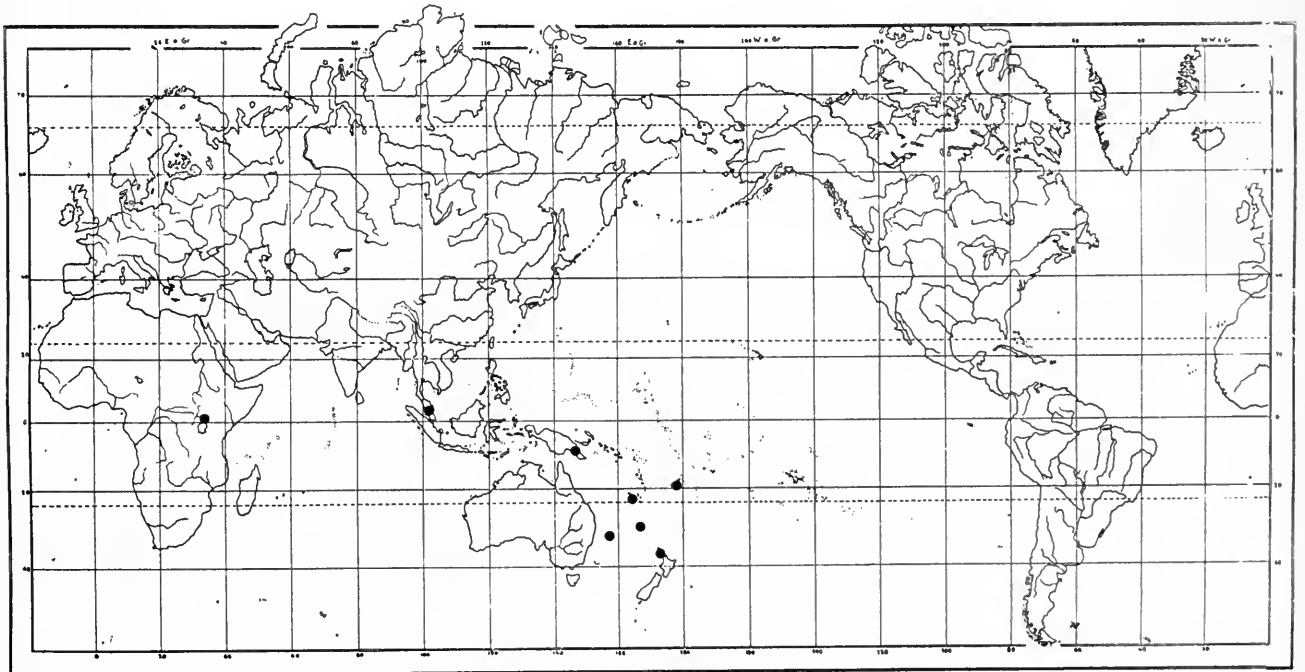


Fig. 23 Distribution of *Pseudocyphellaria poculifera* in the palaeotropics.



Fig. 24 *Pseudocyphellaria prolificans*. Holotype (PC). Scale in mm.

diam., margins raised, projecting from tomentum, decorticate area flat.

Pycnidia common, scattered on upper surface, or concentrated in groups or lines at lobe margins, hemispherical, 0.1 mm diam., ostiole raised, red-brown.

Apothecia rather rare, often absent, when present prominent, marginal or submarginal, rounded 2–4(–5.5) mm diam., subpedicellate, pedicel short, 1–1.5 mm wide, pale whitish buff, exciple pale whitish buff to yellow-brown, translucent when wet, massive, corrugate-scabrid, obscuring disc when young, persisting at maturity as a thick, prominent margin, disc \pm deeply cupuliform at first, subconcave to plane at maturity, smooth, shining, pale to dark chestnut-brown to red-brown, epruinose. *Epithecium* pale yellow-brown, to

14 μ m thick. *Hymenium* colourless, 110–125 μ m tall. *Ascospores* yellow-brown, simple to 1-septate, fusiform-ellipsoid, apices rounded or pointed, 28–33.5 \times 6.5–8 μ m.

CHEMISTRY. Tenuiorin, methyl gyrophorate, gyrophoric and congyrophoric acids, 7 β -acetoxyhopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *Pseudocyphellaria prolificans* is a widespread palaeotropical species having a white medulla; a dimpled, punctate-impressed upper surface, often also conspicuously papillate (use \times 10 lens); conspicuously thickened margins below; scattered to densely clustered and proliferating marginal and laminal phyllidia; a white medulla; a green

photobiont; and a two-hopane chemistry with tenuiorin, and gyrophoric acid and derivatives.

It is distinguished from *P. sulphurea* by the marginal and laminal phyllidia; from *P. insculpta* by the green photobiont; from *P. multifida* by the dimpled, punctate-impressed upper surface, the proliferating phyllidia and thicker margins; and from *P. homalosticta* and *P. reineckeana* in lacking pseudocypHELLAE on the upper surface.

DISTRIBUTION AND ECOLOGY. Widely distributed in the palaeotropics (Fig. 25) from Sri Lanka eastwards to Fiji and Samoa in the south-western Pacific. Also known from north-eastern Australia. On twigs, branches and trunks of trees and shrubs, and on rotting logs in humid montane rainforest and cloudforest, 500–3600 m.

SPECIMENS EXAMINED. **Sri Lanka:** Kandy, *Moon* (BM). **Malaysia:** **Sabah.** Mesilau River, *Hale* 29225 (TNS); Mt Kinabalu, *Samsudin* (UKMB). **Indonesia.** **Sumatra:** Mt Sago near Pajakumbuh, *Meijer* B 8273 (L). **Java:** Tjibodas. Mt Gede, *v. Ooststroom* 14457, 14465, 14597 (Herb. Aptroot); sine loco, *Koernich* s.n. (Herb. Aptroot); Mt Kwai, Mt Panderman, *Groenhart* 2639, 2640 (L); Mt Gegerbentang, [on tree] *Groenhart* 2232 (L); Tjibeureum Falls, *Schiffner* 1575 (L); sine loco, *Junghuhn* (L); Mt Pangerango, *Schiffner* 1155, 2970, 3079 (L, BM, WU); sine loco, *Blume* (L). **Philippines:** **Luzon.** Benguet. Mt Santo Tomas, *Aptroot* 20321, 20392 (Herb. Aptroot). **Mindanao.** Mt Batangan, *Warburg* 14214c (B). **Palawan.** Brookes Point. Mt Mantalin-gahan, *Sipman & Tan* 29978 (B). **Irian Jaya:** *Bamler* s.n. (B); Vogelkop Penin. Nettoti Range. Mt Nettoti, *v. Royen & Sleumer* 7476 (Herb. Aptroot). **Papua New Guinea:** **Eastern Highlands.** Chimbu. Lake Aunde, *v. Balgooy* 316 (Herb. Aptroot); Mt Wilhelm, *Weber & McVean* (Herb. Aptroot); *Aptroot* 31580 (Herb. Aptroot); Bundi Gap, *Aptroot* 32195 (Herb. Aptroot); Kotdame, *Mundua* 214, 220 (CBG); Goroka. Mt Gahavisuki Provincial Park, *Aptroot* 31036

(Herb. Aptroot); track to Mt Michael, *Streimann* 18502, 18541, 18809, 18825 (CBG). **Southern Highlands.** Mt Giluwe, *Lambley* (BM); Onim Forestry Station, *Streimann* 24761 (CBG); Margarima-Tari Road, *Streimann* 24369 (CBG). **Morobe.** Wau, Edy Creek Road, *Sipman* 15619 (Herb. Aptroot); Mt Missim, *Bellamy* 1530 (B); Yinimba, *Streimann* 19135 (CBG); track to Mt Missim, *Bellamy* 202, 202a (CBG); *Streimann* 18772 (CBG); Ekuti Divide, *Rau* 702 (CBG); *Streimann* 20126, 20136 (CBG); Mt Kauwara, *Kairo* 687–8 (CBG); Kaisinik, *Kashiwadani* 10739 (TNS); Araulu Logging Area, *Streimann* 13552 (CBG); Slate Creek & Gumi Creek Divide, *Streimann* 13868 (CBG); Wagau-Mulolo Track, *Streimann* 19615 (CBG); Spreader Divide, *Streimann* 11841, 11900 (CBG); Bulolo-Watutu Divide, *Streimann* 25033 (CBG); Honzeukngon village, *Aptroot* 18024 (Herb. Aptroot). **Milne Bay.** Mt Moiba, *Pullen* 7744 (Herb. Aptroot). **Madang.** Finisterre Range, Teptep Village, *Aptroot* 31959, 31997 (Herb. Aptroot). **Central.** Near Myola, *Lambley* (BM); Mt Albert-Edward, *Kashiwadani* 11523, 11723, 11821, 12011 (TNS); 2 km N. of Waitotape Airstrip, *Kashiwadani* 12100 (TNS). **Western Highlands.** Milep Area, *Vinas* 7647 (CBG). **Solomon Islands:** **Guadalcanal Island.** Mt Popomansiu, *Hill* 9283, 9288, 9513, 9561, 9670, 9687, 9709, 9827, 9841, 9856 (BM); Mt Gallego, *Hill* 8173, 8363 (BM); southern slopes of Mt Makarakomburu, *Glenny* 2048, 2055, 2125 (BSIP). **Kolombangara Island.** Ridge west of Kolombangara River, *Hill* 10544, 10573 (BM). **New Caledonia:** [ISOLECTOTYPE] sine loco, *Vieillard* 1795 (B); Rivière Blanche, *Hill* 11696 (BM). **Kermadecs:** [Raoul] **Sunday Island.** Sine loco, *Milne* (NY). **Fiji:** **Viti Levu.** Sine loco, *Degener* (GZU); ridge between Mt Nanggaranambuluta [Lomalangi] and Mt Namama, *Smith* 5004 (BM, L, US); western slopes of Mt Nanggaranambuluta, east of Nandari-vatu, *Smith* 4818 (US); Mt Evans Range, *Smith* 4280 (BM, US); Mt Victoria, *Green* (BM); *Lam* 6823 (L). **Ngau.** Herald Bay, *Smith* 7828 (US). **Ovalu.** Sine loco, *Gräffe* (W). **Samoa:**

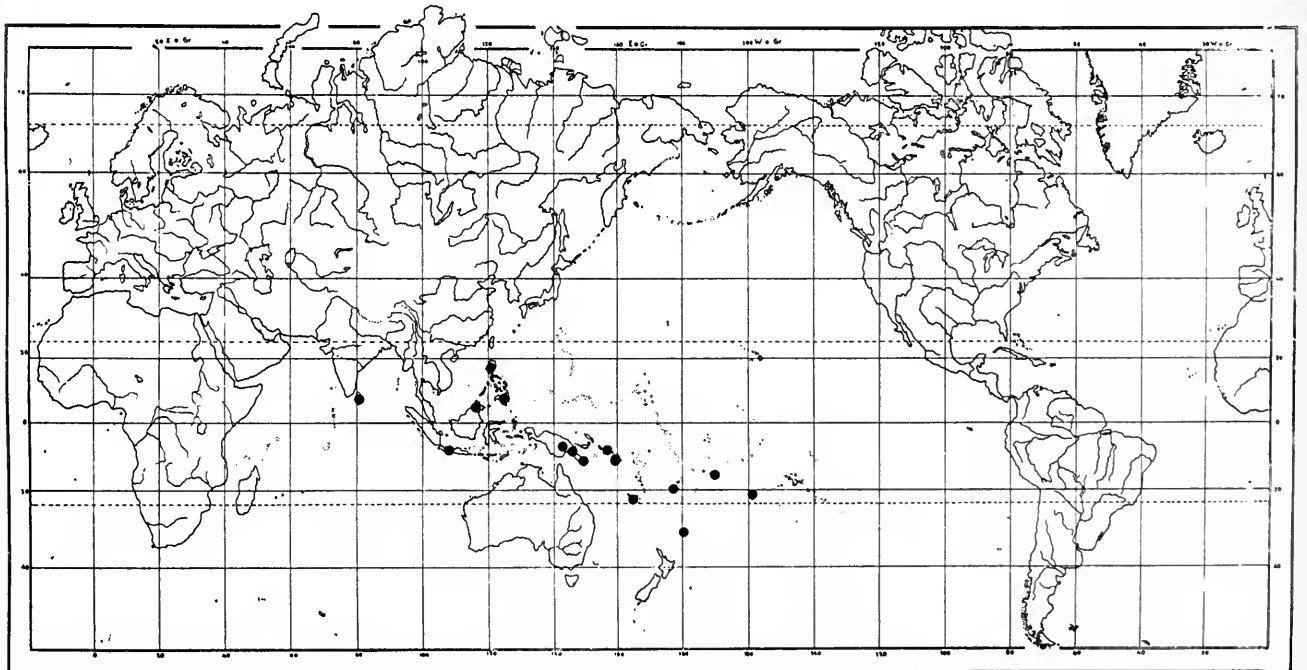


Fig. 25 Distribution of *PseudocypHELLARIA prolifcans* in the palaeotropics.

Upolu. See Lanonmea, *Hochsentimer?* (B). **Rarotonga:** Connells Gully, Parks 22171 (COLO).

23. ***Pseudocyphellaria punctillaris*** (Müll. Arg.) D.J. Galloway in *Graphis Scr.* 5: 9 (1993). *Stictina punctillaris* Müll. Arg. in *Hedwigia* 30: 48 (1891). *Stictina fragillima* f. *punctillaris* (Müll. Arg.) Stizenb. in *Flora, Jena* 81: 129 (1895). *Sticta fragillima* f. *punctillaris* (Müll. Arg.) Zahlbr., *Cat. lich. univ.* 3: 382 (1925). Type: Australia. Queensland, near Mt Bellenden Ker, 'Whelman Pools. Austral. orient', 1889, *F.M. Bailey* 567 (G 002544-holotype).

Fig. 26.

Thallus rosette-forming, 5–10(–15) cm diam., closely attached from margins to centre. *Lobes* broadly rounded, 5–8(–12) mm wide, contiguous or imbricate at margins, crowded-imbricate centrally. *Margins* entire, sinuous, broadly rounded at apices, becoming markedly lobulate-phyllidiate centrally, thickened and sometimes inrolled below. *Upper surface* dark malachite green to glaucous-blue when wet, pale yellowish fawn to brownish or pale red-brown, darker at apices when dry, undulate to wrinkled,

conspicuously verrucose-scabrid (use $\times 10$ lens), thick, coriaceous, without isidia, maculae or soredia. *Phyllidia* marginal, rarely regenerating from cracks on upper surface, 0.2–1.5 mm diam., lobulate, distinctly jointed at base, simple to subcoralloid. *Pseudocyphellae* white, numerous, often crowded, conspicuous, 0.1–0.5 mm diam., round to elongate, conical-verruciform, margins raised, decorticate area flat. *Medulla* white. *Photobiont* cyanobacterial. *Lower surface* pale yellowish white to buff at margins, cinnamon-brown to red-brown centrally, uniformly tomentose from margins to centre, tomentum thick, woolly, pale at margins, brownish or greyish centrally, often obscuring pseudocyphellae. *Pseudocyphellae* white, scattered, round to irregular, 0.1–1 mm diam., most noticeable at margins, decorticate area flat or concave, granular, margins not raised.

Pycnidia common, prominent, swollen, solitary or crowded, marginal and laminal 0.2–1 mm diam., ostiole punctate, red-brown.

Apothecia sparse to frequent, submarginal and laminal, central rarely at lobe apices, sessile, constricted at base, round to deformed through mutual pressure, 1–3 mm diam., shallowly concave to plane, exciple prominent, coarsely

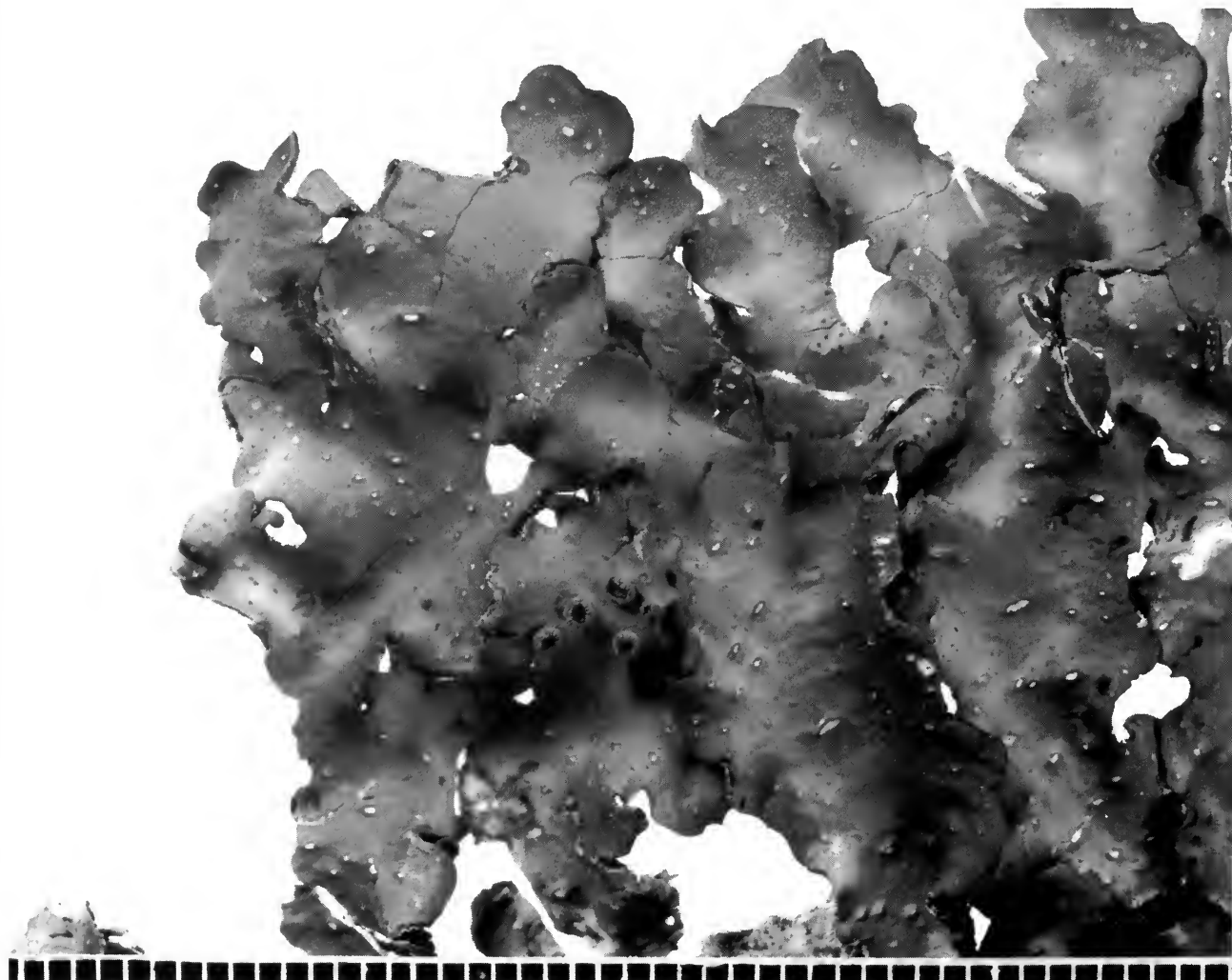


Fig. 26 *Pseudocyphellaria punctillaris*. J.K. Bartlett 32147 (AK, BM). Scale in mm.

verrucose-scabrid, obscuring disc when young, persisting as a coarse, dentate-verrucose margin to disc at maturity, pale brownish, disc shining, slightly roughened, pale to dark red-brown, epruinose. *Epithecium* red-brown, 8–14 μm thick. *Hymenium* colourless, 110–115 μm tall. *Ascospores* 1-septate, contents vacuolate, pale red-brown or yellow-brown, broad-ellipsoid, apices pointed or rounded, 25–28 \times 8.5–11 μm .

CHEMISTRY. Tenuiorin, methyl gyrophorate, gyrophoric acid, 7 β -acetoxyhopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *P. punctillaris* has rather shortly \pm subdichotomously branching lobes with a white medulla, a scabrid-areolate upper surface, a cyanobacterial photobiont and white pseudocyphellae on both upper and lower surfaces. It has a simple two-hopane chemistry with tenuiorin and gyrophoric acid present as accessories. Known from eastern Australia and the Philippines (Galloway & Kemp, 1993). It is distinguished from *P. godeffroyii* by the marginal lobulate phyllidia; and from *P. rigida* (which has a scrobiculate upper surface), *P. semilanata* and *P. trichophora* by its scabrid-areolate upper surface and marginal phyllidia.

DISTRIBUTION AND ECOLOGY. A characteristic Pacific species (Fig. 27) known from Indonesia and New Guinea where it seems to be most commonly collected, also from the Philippines, Samoa and in eastern Australia (Galloway & Kemp, 1993), and a single record from Hawaii. It is an epiphyte of rainforest trees and shrubs with an altitudinal range of 100 to 3650 m. Still rather poorly collected in the region.

SPECIMENS EXAMINED. **Indonesia. Java:** sine loco, sine coll. (L). **Philippines: Luzon.** Mt Makiling, *Degelius* As-704, As-706 (UPS). **Papua New Guinea: Eastern Highlands.** Chimbu. Pindaunde Valley, *Weber & McVean* (Herb.

Aptroot); Felsspitze, *Ledermann* (B); Mt Wilhelm, *McVean* 66179 (CBG); top of Kassam Pass, *Streimann* 17915 (CBG). **Morobe.** Ekuti Divide, *Streimann* 22615 (CBG). **Milne Bay.** Woodlark Island, *Kumei* 34, 41, 95 (CBG); *Soma* 3 (CBG). **Samoa: Savai.** Lake Mafane, *Bartlett* 32147 (AK, BM). **Hawaiian Islands: Hawaii.** Waimea, *Rock* [Sandwicensens No. 6] (B).

24. ***Pseudocyphellaria reineckeana*** (Müll. Arg.) D.J. Galloway in *Lichenologist* 17: 305 (1985). *Stictina reineckeana* Müll. Arg. in Reinecke, *Bot. Jb.* 23: 295 (1896). *Sticta reineckeana* (Müll. Arg.) Zahlbr. in Rech., *Denkschr. Akad. Wiss. Wien* 81: 262 (1907). Type: Samoa, sine loco, 1895, Reinecke (G 002145-lectotype (Galloway, 1985: 305)).

Fig. 28.

Thallus irregularly spreading, 2–4(–8) cm diam., loosely attached centrally, margins \pm free. *Lobes* narrow to medium, (1–)2–4(–8) mm wide, 5–15(–25) mm long, dichotomously to irregularly branching, divergent, discrete at apices, complex-imbriate centrally, apices pointed or smoothly rounded. *Margins* entire, only very slightly thickened below. *Upper surface* bright lettuce green or olive-green suffused brownish when wet, pale glaucous-green to pale buff to dark green-brown when dry, undulate, smooth, to irregularly wrinkled, not faveolate or punctate-impressed, matt or shining, rather brittle, friable when dry, without isidia, maculae, phyllidia or soredia. *Pseudocyphellae* white, scattered, rather sparse, minute, 0.1 mm diam. or less, fleck-like, punctiform, margins not noticeably raised. *Medulla* white. *Photobiont* green. *Lower surface* pale whitish buff to brownish, darkening centrally, smooth or shallowly wrinkled, glossy at margins, thinly to thickly tomentose centrally, tomentum ragged, whitish to pale buff, often inapparent, to thick, black or brown-black, woolly-entangled and obscuring lower surface

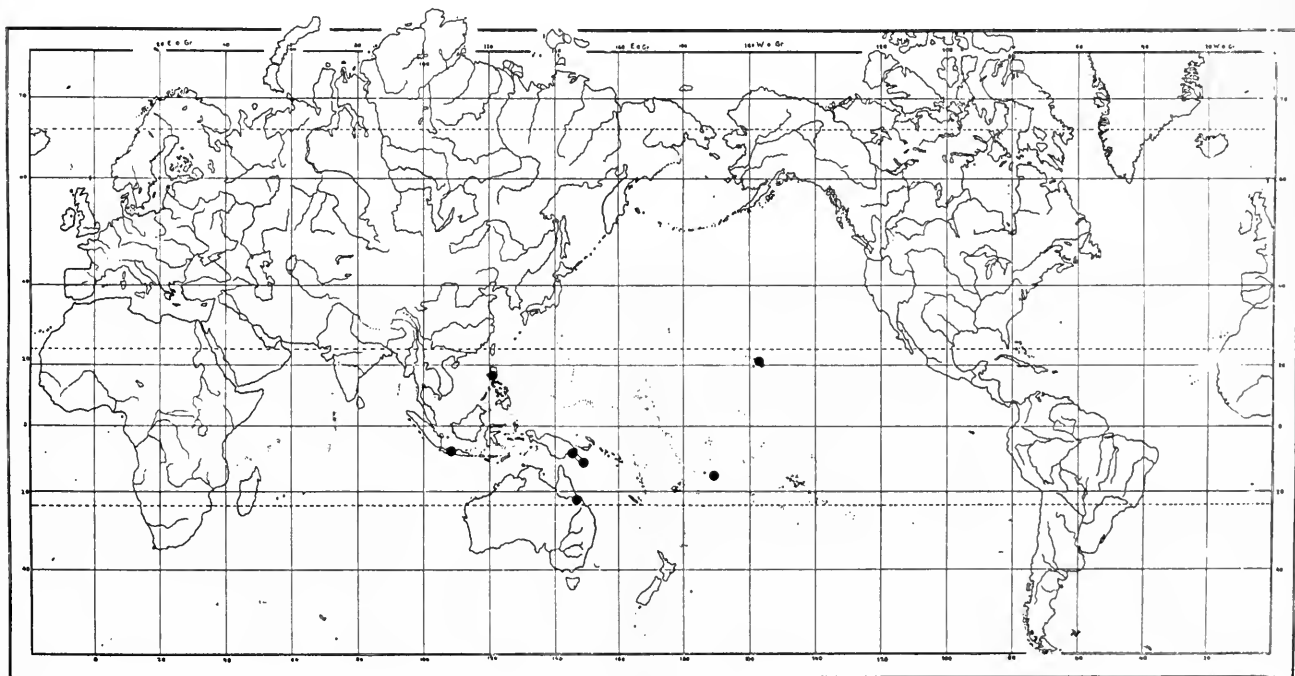


Fig. 27 Distribution of *Pseudocyphellaria punctillaris* in the palaeotropics.



Fig. 28 *Pseudocyphellaria reineckeana*. Lectotype *Sticta reineckeana* (G 002145). Scale in mm.

and pseudocyphellae. *Pseudocyphellae* white, minute, fleck-like, 0.1 mm diam. or less, widely scattered, margins not noticeably raised.

Pycnidia marginal, in groups or lines, minute, punctiform, 0.1 mm diam. or less, ostiole brown-black.

Apothecia rare (often absent) to occasional, marginal or submarginal, sessile, constricted at base, rounded, 0.2–2 mm diam., exciple prominent, coarsely verrucose-scabrid, obscuring disc when young, persisting as verrucose-areolate margin at maturity, pinkish brown, translucent when wet, disc orange to red-brown, shining, epruinose. *Epilhecium* pale yellow-brown, 5.5–9 μm thick. *Hymenium* colourless to pale straw, 85–100 μm tall. *Ascospores* 1-septate, yellow-brown to

red-brown, contents vacuolate, ellipsoid, apices rounded or pointed, 25–31 \times 8.5–11.5 μm .

CHEMISTRY. Methyl gyrophorate, gyrophoric acid (+ to ++), 7 β -acetoxyhopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *Pseudocyphellaria reineckeana* is characterized by rather narrow lobes, a white medulla, a green photobiont, white fleck-like pseudocyphellae on both upper and lower surfaces and rather variable tomentum on the lower surface which varies from thin and scattered or inapparent, to thick and dark and woolly, obscuring the lower

surface. It has a basic two-hopane chemistry with variable amounts of gyrophoric acid which give a characteristic C+ red medullary reaction. It is similar to *P. homalosticta* but lacks the isidia characteristic of that species; it is distinguished from several taxa which have green photobionts and a two-hopane chemistry, from *P. sulphurea* and *P. stenophylla* by lacking a punctate-impressed upper surface and having pseudocyphellae on the upper surface; from *P. homalosticta* in lacking isidia and from *P. prolificans* and *P. multifida* in lacking marginal and laminal lobules or phyllidia.

DISTRIBUTION AND ECOLOGY. An epiphyte of trees and shrubs in montane rainforest, 1000–3500 m. Apparently restricted to the south-west Pacific from Borneo to Samoa (Fig. 29).

SPECIMENS EXAMINED. **Malaysia:** Sabah. Mt Kinabalu, *Samsudin* (UKMB). **Kalimantan.** Sine loco, *Lobb* (BM). **Papua New Guinea: Southern Highlands.** Lai River, *Streimann* 22226 (CBG). **Solomon Islands: Guadalcanal Island.** Mt Popomansiu, *Hill* 9717 (BM). **Fiji: Viti Levu.** Suva, *Wilson* (MEL); Mt Nangaranamuluta [Lomalangi], *Smith* 4833 (US); Mt Victoria, *Green* (BM); Nandarivatu, *Green* (BM); sine loco, *Seeman* (BM). **Vanua Levu.** Mt Kasi, *Smith* 1812 (BM). **Samoa: Savai'i.** *Reinecke* 52a (B).

25. *Pseudocyphellaria rigida* (Müll. Arg.) D.J. Galloway in *Lichenologist* 17: 305 (1985). *Stictina rigida* Müll. Arg. in *Bull. Herb. Boissier* 4: 89 (1896). *Sticta rigida* (Müll. Arg.) Zahlbr., *Cat. lich. univ.* 3: 398 (1925). Type: Australia. Queensland, sine loco, *F.M. Bailey* (G 001990-holotype). Fig. 30.

Thallus rosette-forming to irregularly spreading 5–10(–15) cm diam., loosely to closely attached centrally, margins free. **Lobes** subdichotomously to irregularly branching, 5–10(–15) mm wide, 0.5–3(–6) cm long. **Margins** entire,

sinuous, markedly thickened-ridged below with prominent, projecting white pseudocyphellae. **Upper surface** dark navy blue to glaucous blue-grey when wet, pale glaucous grey or grey-brown when dry, undulate, irregularly wrinkled to shallowly faveolate, interconnecting ridges smoothly rounded, sometimes indistinct, faveolae shallow, rather papery when dry, flabby when wet, without isidia, phyllidia or soredia. **Maculae** white, minute, ± reticulate, best seen when wet at lobe apices (use × 10 lens), more extensive whitish or buff cyanobiont-free areas often seen. **Pseudocyphellae** scattered, on laminal ridges, rather sparse, white, 0.1 mm diam., margins slightly raised. **Medulla** white. **Photobiont** cyanobacterial. **Lower surface** pale whitish buff or ± greyish at margins, slightly darkening centrally, wrinkled-bullate, sparsely tomentose centrally with prominent glabrous margins or tomentose from margins to centre, tomentum dark brown, woolly, entangled. **Pseudocyphellae** scattered, minute, white, rather sparse at margins, prominent centrally, markedly conical-verrucose, margins prominent, swollen, concolorous with lower cortex, 0.5–1 mm diam., projecting above tomentum.

Pycnidia not seen.

Apothecia marginal and laminal, rather sparsely developed in older parts of thallus, sessile to subpedicellate, strongly constricted at base, rounded, 0.5–2.5(–3) mm diam., shallowly concave to plane, ± undulate at maturity, exciple coarsely corrugate-scabrid, pale buff or brown, ± translucent when wet, obscuring disc at first, persisting as a ± thick verrucose-scabrid-dentate margin or sometimes ± occluded by disc, disc pale orange-brown to red-brown, shining when young, matt at maturity, smooth, epruinose. **Epithecium** pale yellow-brown, to 14 µm thick. **Hymenium** colourless, 85–100 µm tall. **Ascospores** pale yellow-brown to red-brown, 1–3-septate, contents often vacuolate, ellipsoid, apices rounded or pointed, (25–)28–30.5(–33.5) × 8.5–11 µm.

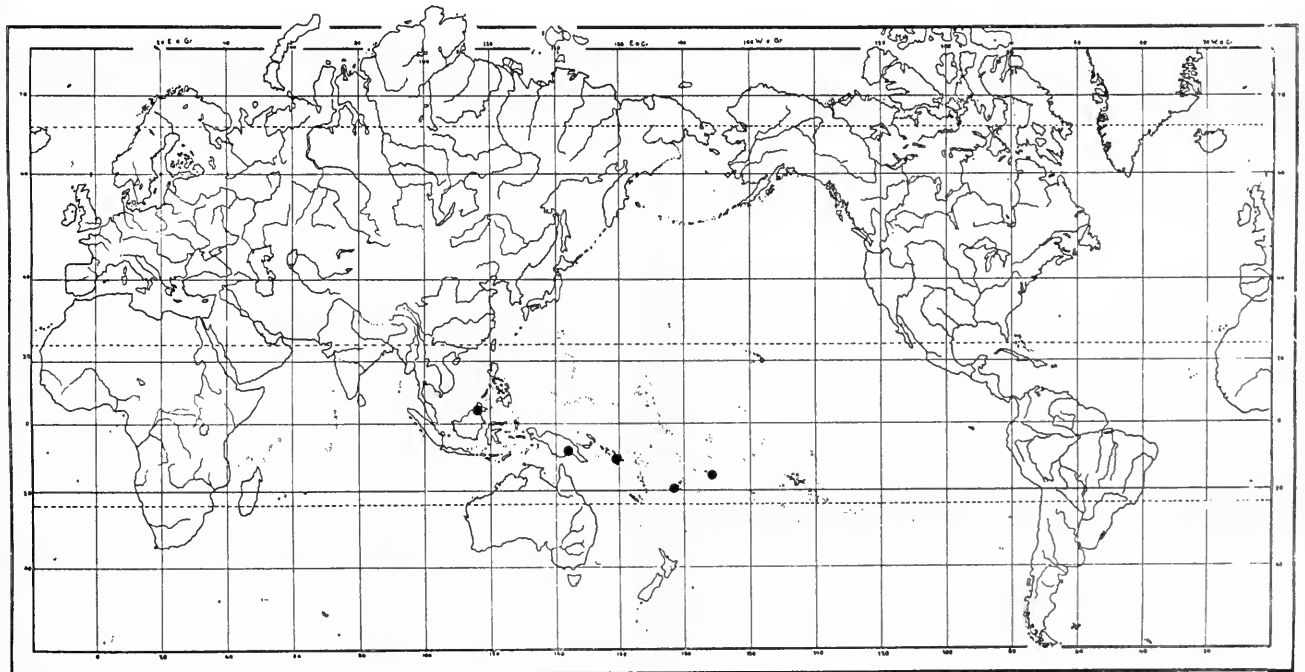


Fig. 29 Distribution of *Pseudocyphellaria reineckeana*.

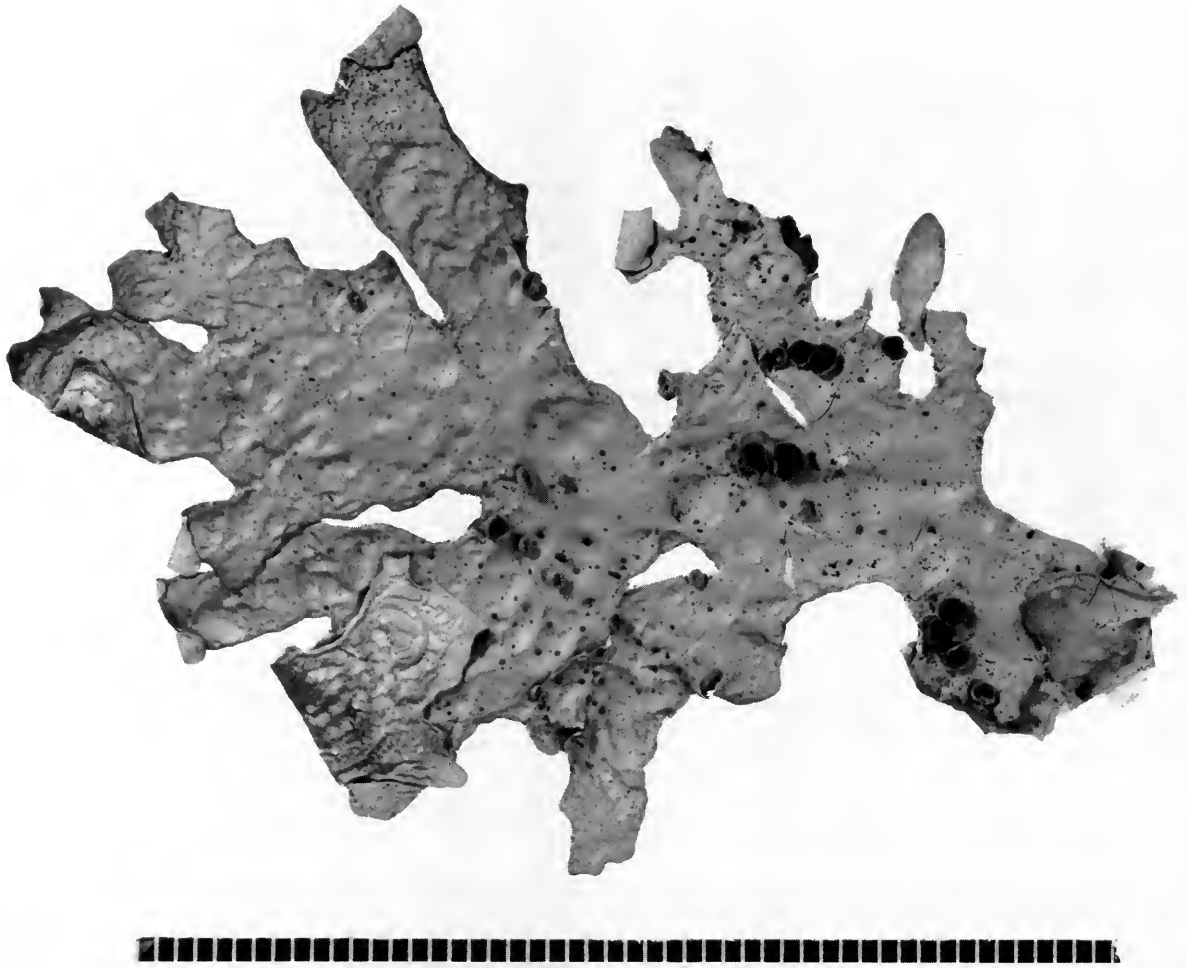


Fig. 30 *Pseudocyphellaria rigida*. H. Kashiwadani 10920 (TNS). Scale in mm.

CHEMISTRY. 7β -acetoxyhopane-22-ol, hopane- 7β , 22-diol (tr.), hopane- 15α , 22-diol.

OBSERVATIONS. *Pseudocyphellaria rigida* is a palaeotropical species characterized by a white medulla, a cyanobacterial photobiont, white pseudocyphellae on both upper and lower surfaces, a scrobiculate-faveolate to punctate-impressed upper surface and a bullate lower surface with continuous to sparse dark tomentum. It has a basic two-hopane chemistry. The distinctive scrobiculate upper surface and rather irregular lobes distinguish *P. rigida* from *P. trichophora* which has a smooth upper surface and hairy lobe margins, and from *P. semilanata* which has a punctate-impressed upper surface and \pm dichotomously branching lobes.

DISTRIBUTION AND ECOLOGY. To date known in the region only from Mt Wilhelm in Papua New Guinea, on tree bark, 3400–3650 m. Known also from north-eastern Australia.

SPECIMENS EXAMINED. **Papua New Guinea: Western Highlands.** Mt Wilhelm en route from Kombugomanbuno to the Pindaude Lakes, Kashiwadani 10920, 10929 (TNS); van Balgooy 593 (Herb. Aptroot).

26. *Pseudocyphellaria semilanata* (Müll. Arg.) D.J. Galloway in *Lichenologist* 17: 306 (1985). *Stictina semilanata* Müll. Arg. in *Bot. Jb.* 23: 293 (1897). *Sticta semilanata* (Müll. Arg.) Zahlbr., *Cat. lich. univ.* 3: 398 (1925). *Cyanisticta semilanata* (Müll. Arg.) Szatala in *Annls hist.-nat. Mus. natn. hung.* 7: 41 (1956), comb. inval. Type: Ins. Samoa, Dr Reinecke (G 002164-holotype).

Fig. 31.

Cyanisticta semilanata var. *epunctulata* Szatala in *Annls hist.-nat. Mus. natn. hung.* 7: 41 (1956). Type: New Guinea, in m. Sattelberg, K. Weinland (B-holotype).

Pseudocyphellaria argyracea var. *reveniensi* Vain. in *Hedwigia* 38: 121 (1913). Type: Philippines, Luzon, Sorsogon, Albay, June 1908, H.M. Curran (TUR-V 10134-holotype).

Thallus irregularly spreading, 8–12(–15) cm diam., loosely attached centrally, apices \pm ascending. *Lobes* very variable, 4–10 mm wide, 1–4(–6) cm long, dichotomously branching, apices divergent, furcate, pointed or rounded, discrete from margins to centre or complex-imbricate centrally, flat to \pm canaliculate. *Margins* entire, distinctly ridged above and

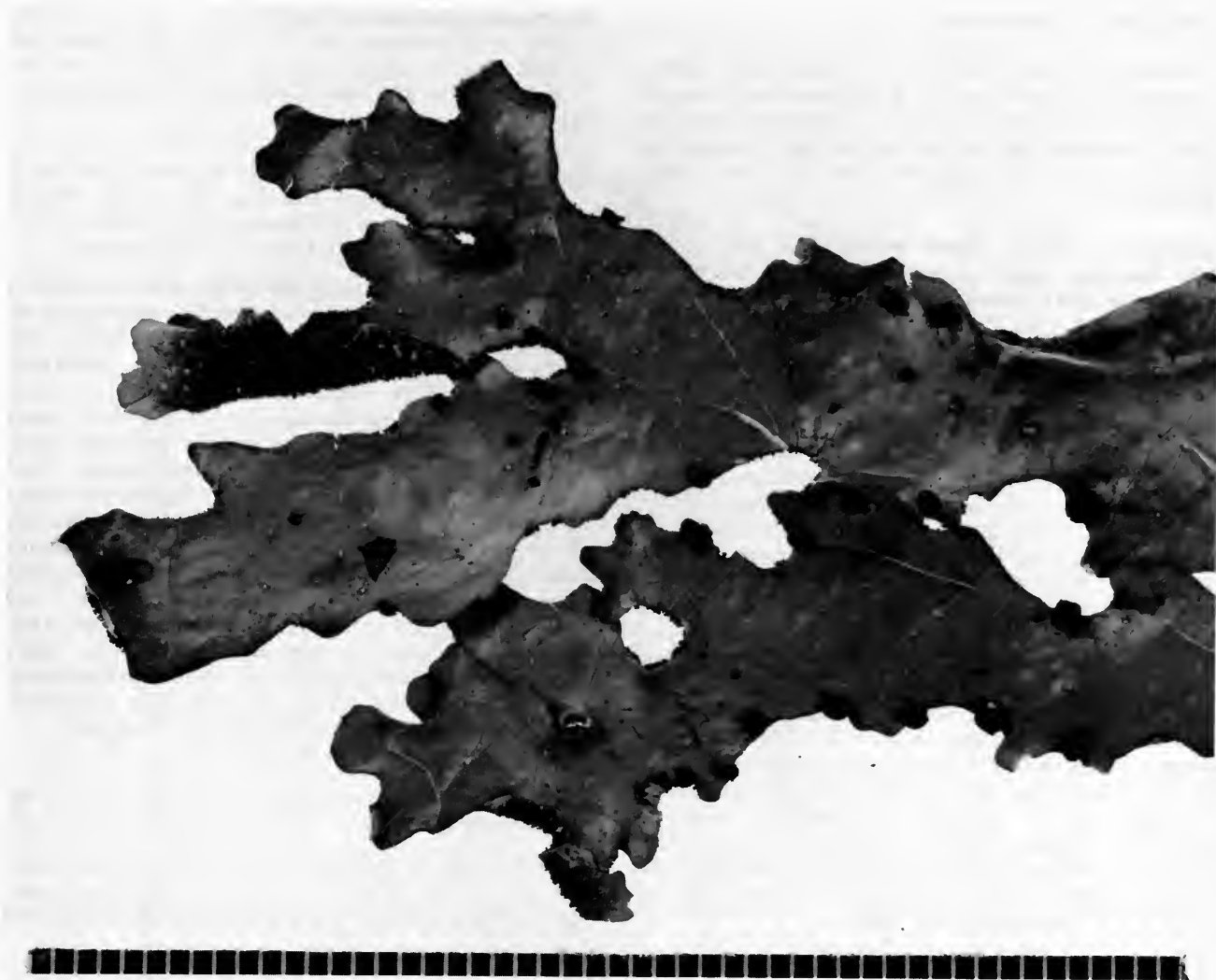


Fig. 31 *Pseudocyphellaria semilanata*.L. Brako 4256 (NY). Scale in mm.

below with often prominent tomentum from lower surface projecting at right angles. *Upper surface* dull slate-blue to glaucous green suffused red-brown in parts especially at margins and apices, pale olivaceous to brownish when dry, undulate, shallowly ridged to distinctly punctate-impressed, rigid, rather coriaceous when dry, pliable when wet, without isidia, phyllidia or soredia. *Maculae* minute, white, imparting a delicate marbling to upper surface (use $\times 10$ lens), prominent, larger and \pm reticulate at lobe apices. *Pseudocyphellae* white, scattered, minute, punctiform, 0.1–0.2 mm diam. *Medulla* white. *Photobiont* cyanobacterial. *Lower surface* yellowish white or pale buff at margins, darkening to red-brown centrally, tomentose from margins to centre, tomentum very thick, entangled, woolly, whitish to red-brown or \pm blackened. *Pseudocyphellae* white, prominent, scattered, round to irregular, 0.2–2 mm diam., margins swollen, prominent, concolorous with lower cortex, often sunk in tomentum.

Pycnidia marginal, hemispherical, 0.1 mm diam., solitary or in groups, ostiole dark red-brown or blackened.

Apothecia marginal or submarginal, rarely laminal, rare (often absent) to occasional, sessile, constricted at base,

rounded, 0.5–2 mm diam., subconcave to plane, exciple prominent in young fruits, persistent to occluded at maturity, slightly roughened to coarsely scabrid-verrucose, pale brownish, translucent when wet, disc pale to dark red-brown, smooth, epruinose, sometimes with a small central thalline lobule of sterile tissue. *Epithecium* pale red-brown, 8.5–14 μm thick. *Hymenium* colourless, 70–85 μm tall. *Ascospores* pale yellow-brown to red-brown, 1–3-septate, fusiform-ellipsoid, (25–)30.5–33(–36) \times 5.5–8 μm .

CHEMISTRY. Methyl gyrophorate (\pm), gyrophoric acid (\pm to ++), 7 β -acetoxyhopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol.

OBSERVATIONS. *Pseudocyphellaria semilanata* is characterized by dichotomously branching lobes, a cyanobacterial photobiont, a white medulla, scattered white pseudocyphellae on both upper and lower surfaces, a punctate-impressed upper surface and a two-hopane chemistry. It is similar to *P. beccarii* but is distinguished from it by having punctiform white pseudocyphellae on the upper surface. It differs from *P. godeffroyii* in having a shining, dimpled upper surface

which is never scabrid-areolate.

DISTRIBUTION AND ECOLOGY. A palaeotropical species occurring in the Pacific from the Bonin Islands and Indonesia eastwards to Fiji and Samoa (Fig. 32). Epiphytic on trees and shrubs, on rotting logs and on litter in upper montane and cloud forest, and on small cut trees and fence posts; 100–3650 m.

SPECIMENS EXAMINED. **Bonin Islands:** sine loco, *Wright* (US). **Indonesia. Java:** *Laurer* s.n. (B); Mt Lawu, *Feekes* 4969 (L); Mt Kawi, *Groenhart* 1828 (L); Mt Ardjuno, *Groenhart* 1517, 7244, 7246, 7247 (L). **Flores:** sine loco, *Verheijen* 5202 (Herb. Aptroot). **Irian Jaya:** sine loco, *Bamler* (B); Biri, *Weinland* (B). **Papua New Guinea: Madang.** Finisterre Mountains, Saidor Subdistrict, Naho-Rawa Div., *Jermy* 4014 (BM). Northern Distr., Tufi subdistr., Lake Ridubidubina, *Hoogland* 4495 (L). **Eastern Highlands.** Chimbu, Pindaunde Valley, *Aptroot* 31382 (Herb. Aptroot); Lake Aunde, 3600 m, *v. Balgooy* 316 (Herb. Aptroot); Mt Wilhelm, *Kashiwadani* 10881, 10883, 10915, 10919, 10937, 10953–4, 10957, 11079, 11081, 11168, 11391, 11411 (TNS); Imbuka Ridge, *Weber & McVean* (COLO). **Morobe.** Saruwaged Range, *Sipman* 24383, 24470 (B); near Honzeukngon village, *Aptroot* 17851, 18018, 18020, 18022 (Herb. Aptroot); Herzog Mountain, *Streimann & Umba* 11032 (CBG). **Southern Highlands.** Iaro River, *Streimann* 23824 (CBG). **Western Highlands.** Nebilyer River, 2760 m, *Streimann* 20600 (CBG); Milne Bay. Woodlark Island, *Kumei* 43–4 (CBG). **Solomon Islands: Guadalcanal.** Mt Popomansiu, *Hill* 9403, 9617 (BM). **Fiji: Viti Levu.** Naitasiri, northern portion of Rairaimatuku Plateau between Mt Tomanivi and Nasonggo, *Smith* 5755 (BM, L, US). **Samoa: Upolo.** Lake Lanoto'o, *Schultz-Motel* 3425 (B); mountains east of Tiave, *Schultz-Motel* 4042 (B); Lanotoo, *Rechinger* 3100 (W). **Savai'i.** Lake Mafane, *Bartlett* 32149, 32153, 32155, 32156 (AK, BM).

27. *Pseudocyphellaria stenophylla* (Müll. Arg.) D.J. Galloway in *Lichenologist* 17: 306 (1985). *Sticta stenophylla* Müll. Arg. in *Flora, Jena* 65: 293 (1897). Type: New Caledonia, Mt Mu, 1886, *Vieillard* (G 002010-holotype). Fig. 33.

Pseudocyphellaria prolificans var. *angustata* Räsänen in *Suomal. elain-ja kasvit. Seur. van. kasvit. Julk.* 20(3): 16 (1944). Type: New Caledonia, ad corticem arboris, 1863(–64), *E. Vieillard* (H-lectotype, selected here).

Thallus irregularly spreading, often rather sparse, 2–4(–6) cm diam, loosely to closely attached centrally, margins free and \pm ascending. *Lobes* very narrow, 0.1–0.5(–1.5) mm wide, 2–8(–15) mm long, irregularly linear-laciniate, subdichotomously to irregularly branching, \pm free at apices, entangled centrally, plane to canaliculate (most noticeable in young, marginal parts). *Margins* entire, slightly thickened above, without isidia, phyllidia, pseudocyphellae or soredia. *Upper surface* bright lettuce green when wet, pale green-grey to pale olivaceous buff when dry, fragile, rather brittle when dry, pliable when wet, without isidia, maculae, phyllidia, pseudocyphellae or soredia. *Medulla* white, photobiont green. *Lower surface* pale whitish buff at margins to pale yellow-brown or red-brown centrally, glossy, glabrous or very sparsely and minutely tomentose in central parts, with a narrow, raised midrib in older parts. *Pseudocyphellae* white, rounded, punctiform, 0.1 mm or less, most common at margins, rather sparse and widely scattered centrally.

Apothecia and pycnidia not seen.

CHEMISTRY. 7 β -acetoxyhopane-22-ol, hopane-7 β , 22-diol (tr.), hopane-15 α , 22-diol and gyrophoric acid.

OBSERVATIONS. *Pseudocyphellaria stenophylla* is characterized by a white medulla; scattered, fleck-like, white pseudocyphellae on the lower surface but not present at the

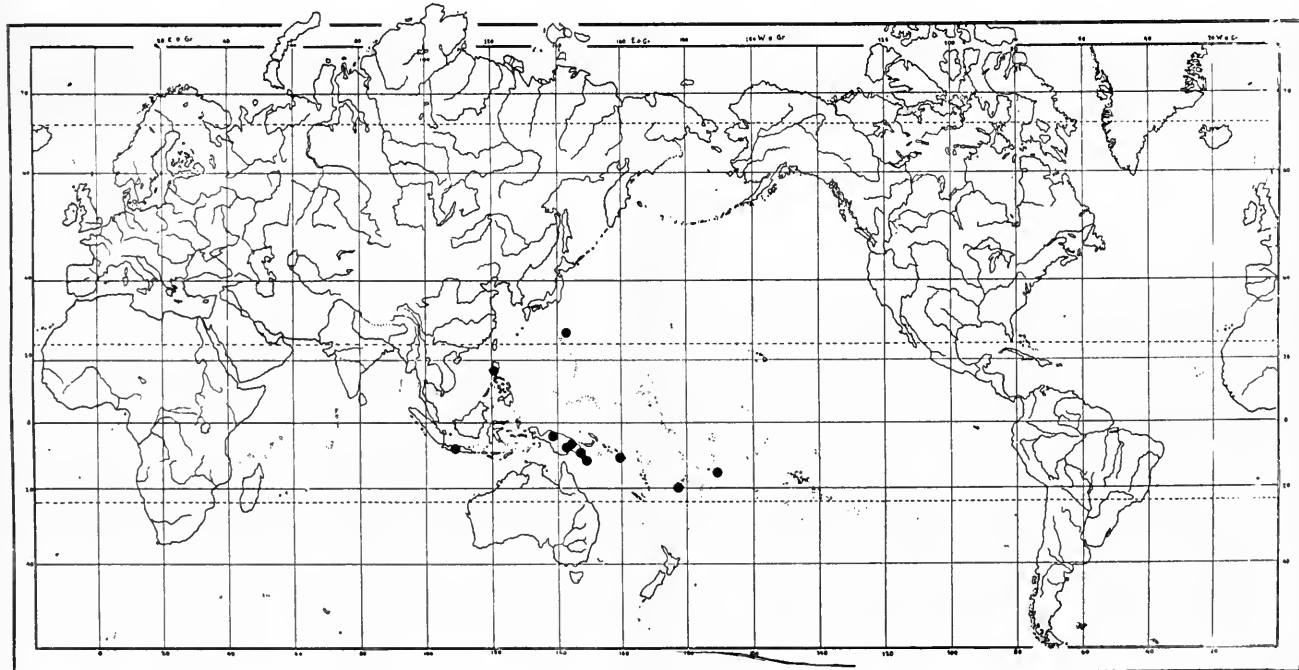


Fig. 32 Distribution of *Pseudocyphellaria semilanata*.



Fig. 33 *Pseudocypbellaria stenophylla*. Holotype (G 002010). Scale in mm.

margins; a green photobiont; a naked lower surface which is \pm costate centrally; very narrow lobes which are subdichotomously to intricately branched; and unthickened margins which are neither isidiate nor phyllidiate. It has a two-hopane chemistry with gyrophoric acid. Its very narrow lobes distinguish it from *P. sulphurea*.

DISTRIBUTION AND ECOLOGY. Known in the region only from the type collections in New Caledonia. Also in Australia (Queensland).

SPECIMENS EXAMINED. **New Caledonia:** known only in the region from the type specimens (see above).

28. *Pseudocypbellaria sulphurea* (Schaer.) D.J. Galloway in *Lichenologist* 17: 306 (1985). *Sticta sulphurea* Schaer. in Moritzi, *Syst. Verz.*: 127 (1846). Type: Java, sine loco, Zollinger 1860x (L 910, 182–20-lectotype (Galloway, 1985b: 306)).

Fig. 34.

Sticta richardi var. *impressa* Meyen & Flot. in *Nova Acta Acad. Leop. Carol.* 19, Suppl.: 216 (1843). Type: Manillae, ad truncos sylvarum, ad Meyen (L 019,211–1788-lectotype (Galloway, 1985: 306)).

Sticta quercifolia Taylor in *Lond. J. Bot.* 6: 177 (1847).

- Pseudocyphellaria quercifolia* (Taylor) Vain. in *Philipp. J. Sci. sect. C, Bot.* **8**: 117 (1913). Type: Sri Lanka, sine collectoribus nomine, no. 40, ex Herb. Hook. (BM-holotype; H-isotype).
- Sticta dissimulata* Nyl., *Syn. meth. lich.* **1**(2): 362 (1860). *Crocodia dissimulata* (Nyl.) Trevis., *Lichenotheca veneta* exs. 75 (1869). *Lobaria dissimulata* (Nyl.) Kuntze, *Revis. gen. pl.* **2**: 876 (1891). *Pseudocyphellaria dissimulata* (Nyl.) Vain. in *Philipp. J. Sci. Sect. C, Bot.* **8**: 118 (1913). Type: Java, sine loco, sine collectoribus nomine (H-NYL 33517-lectotype (Galloway, 1985b: 307)).
- Sticta punctulata* Nyl., *Syn. meth. lich.* **1**(2): 364 (1860). *Crocodia punctulata* (Nyl.) Trevis., *Lichenotheca veneta* exs. 75 (1869). *Lobaria punctulata* (Nyl.) Kuntze, *Revis. gen. pl.* **2**: 876 (1891). Type: Java, sine loco, Zollinger 1799 pr.p. (H-NYL 33481-lectotype (Galloway, 1985b: 307)).
- Sticta demutabilis* Kremp. in *J. Mus. Godeffroy* **1**(4): 98 (1874). *Pseudocyphellaria demutabilis* (Kremp.) Gyeln. in *Revue bryol. lichén.* **6**: 173 (1933). Type: Samoa, Savai, mont. veg ad arbores, *E. Gräffe* 106 (M-holotype; W-isotype).
- Sticta demutabilis* f. *laevis* Kremp. in *J. Mus. Godeffroy* **1**(4): 98 (1874). *Pseudocyphellaria dissimulata* var. *laevis* (Kremp.) Szatala in *Annlis hist.-nat. Mus. natn. hung.* **7**: 40 (1956), comb. inval. (Art. 33.2). Type: Samoa, Ins Upolu, *E. Gräffe* 101 (M-lectotype (Galloway, 1985b: 307)).
- Sticta demutabilis* f. *minor* Kremp. in *J. Mus. Godeffroy* **1**(4): 98 (1874). Type: Samoa, Savai, *E. Gräffe* 109 (M-holotype).
- Sticta karstenii* Müll. Arg. in *Flora, Jena* **64**: 505 (1881). *Pseudocyphellaria karstenii* (Müll. Arg.) Szatala in *Annlis hist.-nat. Mus. natn. hung.* **7**: 40 (1956), comb. inval. (Art. 33.2). Type: Novae Hollandiae [Australia], North Queensland, Bellenden Ker Range, *Karsten* 2, comm. F.v. Mueller 1881 (G 002020-holotype).
- Sticta leucophylla* Müll. Arg. in *Flora, Jena* **72**: 506 (1889). *Pseudocyphellaria leucophylla* (Müll. Arg.) Szatala in *Annlis hist.-nat. Mus. natn. hung.* **7**: 39 (1956), comb. inval. (Art. 33.2). Type: New Guinea, near summit of Owen Stanley Range, *Sir W. Macgregor* 6 pr.p., comm. F. v. Mueller 1889 (G 002116-holotype).
- Pseudocyphellaria dissimulata* var. *hypophaea* Vain. in *Philipp. J. Sci. Sect. C, Bot.* **8**: 118 (1913). Type: Philippines, Mindanao, District of Zamboanga, ± 1200 m alt., on trees, Nov.–Dec. 1911, *E.D. Merrill* 8351 (TUR-VAINIO 10195-lectotype, selected here).
- Pseudocyphellaria dissimulata* var. *nudior* Vain. in *Philipp. J. Sci. Sect. C, Bot.* **8**: 118 (1913). Type: Philippines, Negros, Canlaon Volcano, 5000 ft, on trees, April 1910, *E.D. Merrill* 6889 (TUR-VAINIO 10191-lectotype, selected here).
- Pseudocyphellaria dissimulata* var. *curranii* Vain. in *Philipp. J. Sci. Sect. C, Bot.* **8**: 119 (1913). Type: Philippines, Luzon, Prov. of Pampanga, Mt Arayat, ad truncum arboris, March 1910, *H. M. Curran* 19341 (TUR-VAINIO 10193-holotype).
- Thallus* irregularly spreading, often in large, entangled clones, 10–20(–35) cm diam., loosely attached centrally, apices free, ± ascending. *Lobes* very variable (1–)3–8(–12) mm wide, (1–)2–8(–12) cm long, linear-elongate, ± dichotomously branching, contiguous or discrete, apices usually free, ± divergent, rounded, pointed, truncate or furcate, complex-

entangled-imbricate centrally. *Margins* entire, smoothly rounded, conspicuously thickened-ridged above and below, here and there with occasional white pseudocyphellae. *Upper surface* bright lettuce-green when wet, occasionally suffused red-brown at apices and margins, pale grey-green, olivaceous to fawnish or red-brown when dry, shining, conspicuously dimpled, punctate-impressed to ± shallowly faveolate, smooth in parts or faveolate but generally strongly punctate-impressed, tough, coriaceous to thin and somewhat papery, without isidia, maculae, phyllidia, pseudocyphellae or soredia. *Medulla* white. *Photobiont* green. *Lower surface* pale whitish to pale yellow-brown or pinkish buff, noticeably wrinkled-ridged, thinly tomentose from margins to centre or ± glabrous, tomentum short, velvety to wispy, whitish to pale buff. *Pseudocyphellae* common, scattered, white, fleck-like, minute at margins, round to irregular centrally, to 0.5 mm diam., margins very slightly raised, concolorous with lower surface, decorticate area flat.

Pycnidia frequent to somewhat sparse, mostly marginal in short lines or in clusters, punctate, 0.1 mm diam. or less, ostiole red-brown to black.

Apothecia absent to occasional to ± frequent, marginal and submarginal, sessile, constricted at base, rounded, 0.5–2.5(–4.5) mm diam., exciple pale pinkish fawn to yellow-brown, translucent when wet, persistent, coarsely scabrid-areolate, disc subconcave to plane, smooth, matt, pale to dark red-brown, epruinose. *Epithecium* pale yellow-brown, 9–15 µm thick. *Hymenium* colourless, 70–95 µm tall. *Ascospores* 1-septate, yellow-brown to red-brown, fusiform-ellipsoid, (22–)25–28(–30.5) × 6.5–8(–11) µm.

CHEMISTRY. 7β-acetoxypopane-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol as constant compounds, with or without some or all of the following as accessory compounds: tenuiorin, methyl gyrophorate, gyrophoric and congyrophoric acids (specimens with gyrophoric acid in quantity give a positive C+ pink medullary reaction).

OBSERVATIONS. *Pseudocyphellaria sulphurea* is a widespread palaeotropical species having a white medulla, a dimpled, punctate-impressed upper surface (not or very rarely truly faveolate) with conspicuously thickened margins below, and scattered, fleck-like, white pseudocyphellae on the lower surface.

In Schaerer's description of *Sticta sulphurea* he mentions '... intus sulphureis' (i.e. yellow medulla) in the account of specimen Zollinger 1860x on which he based the name. However, examination of authentic Zollinger material from Java bearing this number failed to reveal any yellow medulla and it is not clear why Schaerer mentioned *sulphureis* in his description. The Zollinger material which bears Schaerer's name has a uniformly white medulla, characteristic of the species, but on all other counts the material fits Schaerer's description precisely.

P. sulphurea is distinguished from *P. stenophylla* by its wider lobes which are thickened at the margins of the lower surface; from the New Zealand endemic *P. rufovirescens* by the characteristic punctate-impressed, dimpled upper surface and the presence of the depside gyrophoric acid; from *P. prolificans* and *P. multifida* by lacking marginal or laminal phyllidia, isidia or proliferations; and from *P. beccarii* which has a similar morphology but has a cyanobacterial photobiont. Photosymbiodemes of *P. sulphurea* and *P. beccarii*, although reported in the literature (James & Henssen, 1976)

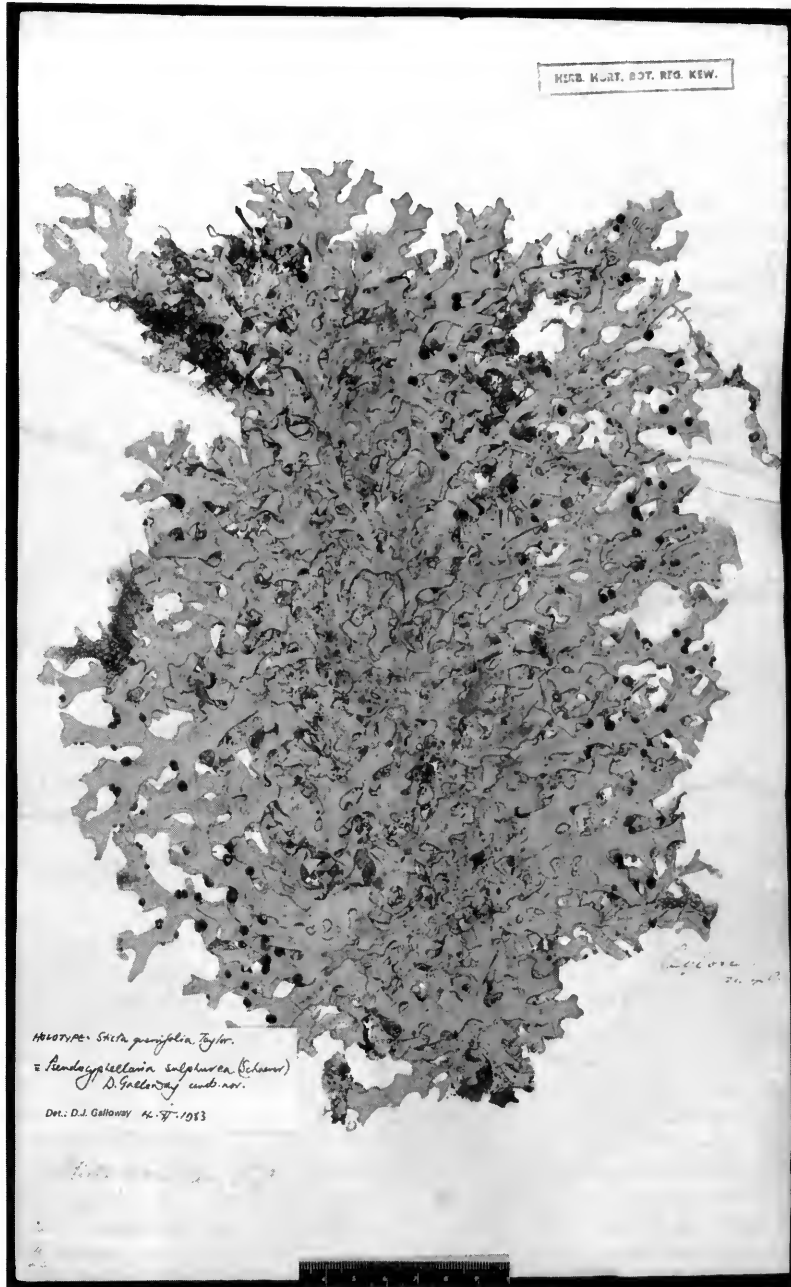


Fig. 34 *Pseudocypbellaria sulphurea*. Holotype *Sticta quercifolia* (BM). Scale in mm.

have not been seen by the present author.

DISTRIBUTION AND ECOLOGY. One of the most common and widespread of palaeotropical lichens (Fig. 35) growing as an epiphyte of branches and trunks of trees and shrubs in dense, humid, mossy montane forest and cloud forest, often forming large mats, also on scattered subalpine trees and shrubs in alpine grassland, 700–3600 m.

SPECIMENS EXAMINED. **Madagascar:** Ambohinutombo forest, *Forsyth Major* 457 (BM); Toshimaniko forest, *Forsyth Major* 96 (BM). **Sri Lanka:** Kandy, *Moon* (BM); sine loco, *Macrae* 131 (BM); Central Province, *Thwaites* C.L. 22 (BM). **Thailand:** Prov. Nakawng Li Thammarat, Khao Luang, *van Beusekom* s.n. (Herb. Aptroot). **Malaysia:** Pahang. Gunong

Hyan, Perak, *Wray* (BM). **Singapore.** Sine coll. 6689 (BM). **Sabah.** Mt Kinabalu, near HQ of National Park, *Ding Hou* 207 (Herb. Aptroot); Mt Kinabalu, *Sipman & Tan* 31085, 31377a (B); 3000 m, *Polak* (B); *Lee* (COLO); Mesilau River, *Hale* 28113, 29194, 29256, 29290 (TNS). **Indonesia.** **Sumatra:** Mt Korinchi, 7300 ft, *Robinson & Kloss* (W); sine loco, *Korthals* (L); sine loco, *Forbes* (BM). **Java:** Salang, v. *Goebel* (M); Prov. Batavia, in monte Megamendong, *Schiffner* 3386 c (M, W); Pamaboela bei Toegoe, *Kurz* (M); Mt Ardjuno, trail from Sumber Brantas Estate to Mt Kembar, *Groenhart* 9856 (Herb. Aptroot); Mt Gede, Tjibodas, *Groenhart* 1807 (L); sine loco, *Weiss* 4517 (B); sine loco, *Laurer* (B); *Junghuhn* (B); Malang, *Lederer* (B); Palang, v. *Goebel* (W); sine loco, *Reinwandt* (B). Mt Gede, *Palmer & Bryant* 1091, 1242 (US);

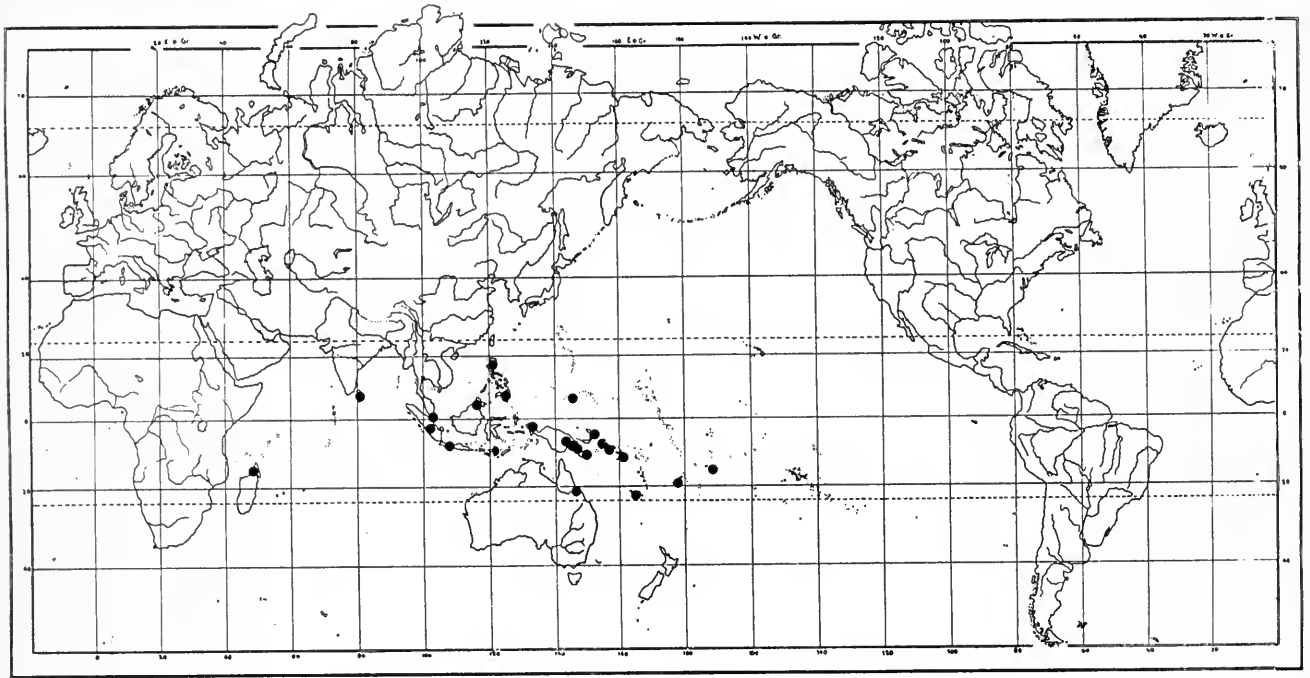


Fig. 35 Distribution of *Pseudocypbellaria sulphurea* in the palaeotropics.

Flores: sine loco, 1970, *J.A.J. Verheijen* 2729 (Herb. Aptroot). **Philippines: Mindanao.** *Elmer* [Kryptogamae exsiccatae editae a Mus. Hist. Nat. Vindobon. 2841] (M, B); Mt Batangan, *Warburg* 14214a (B); Mt Apo, *Mearns* s.n. (US); Davao. Mt Apo, *Elmer* 11535 (W); sine loco, *Mearns* s.n. (W); *Elmer* (BM, W). **Luzon.** Benguet, Baguio, *Elmer* 83; Pampanga. Mt Pinatubo, *Elmer* 21939 (B); Benguet. Baguio, *Elmer* s.n. (US); Mt Tonglon, *Ramos* s.n. (US); *Curran* s.n. (US); ?Fayobos. Mt Banohas, *Elmer* 7565 (W). **Mindoro.** Mt Halcon, *Sales & Wijangco* 10 (B); *Merrill* s.n. (US). **Camarines.** Mt Isarog, *Ramos* 6042 (BM). **Caroline Islands: Ponape.** Mt Erica, *Cheatham* 27 (B); Mt Tamantamansakir, *Glassman* (W). **Irian Jaya: Vogelkop Peninsula, Tamrau Range, Gunung Bagimana, van der Zon s.n. (Herb. Aptroot); Vogelkop Peninsula, Nettoti Range, Wekari River camp, *van Royen & Sleumer* 8145 (Herb. Aptroot). **Papua New Guinea: East Sepik.** Kairuru Island, *Borrell* 3 (CBG). **Madang.** Huon Peninsula, Finisterre Range, Yupna Valley, Teptep Village, trail NNW towards Bambu, *Aptroot* 31919, 32000, 32009 (Herb. Aptroot). **Morobe.** Track to Mt Missim, *Broome* 89A, 208 (CBG, B); *Bellamy* 201, 202b, 204a, 207–8, 208a, 1392, 1453 (B); *Streimann* 18511 (CBG); Mt Sarawaket [Saruwaged] Southern Range, *Koponen* 32872 (Herb. Aptroot); Monkumbion, *Hoogland* 9764 (BM); Cromwell Mountains, *Koponen* 31200 (Herb. Aptroot); Spreader Divide, *Schodde & Craven* 4944 (Herb. Aptroot); Edie Creek Road, *Sipman* 15621 (B); Skindiwai, *Kairo* 391 (CBG); Ekuti Divide, *Rau* 697, 701, 704–5 (CBG); Kauwara River, *Kairo* 670, 672 (CBG); Eraulu Logging Area, *Kairo* 318 (CBG); Mt Missin, *Kashiwadani* 10405, 10410 (TNS); Mt Kaindi, *Kashiwadani* 10454 (TNS); *Streimann* 24817, 33281 (CBG); 7 km SE of Bulolo, *Kashiwadani* 10808 (TNS); Herzog Mountains, *Streimann & Umba* 10962, 11100 (CBG); Gumi Divide, *Streimann* 22712 (CBG). **Southern Highlands.** Tari, Mt Ne, *Kalkman* 4866 (Herb. Aptroot); Tari Gap, *Lambley* (BM); Lama Sawmill Logging Area, *Streimann***

24710 (CBG); Munia Logging Area, *Streimann* 23212 (CBG). **Eastern Highlands.** Chimbu, Imbuka Ridge, *Weber & McVean* (Herb. Aptroot); track to Mt Wilhelm, *Sipman* 21922, 21929 (B); Mt Wilhelm, *Borgmann* 719, 732, 805 (B); *Kashiwadani* 10838, 10847, 10867, 10890, 10944, 10961, 11038, 11187, 11195, 11206, 11349, 11414 (TNS); near Hogabi Village, *Streimann* 18615, 18662, 18694 (CBG); track to Mt Michael, *Streimann* 18789, 18828 (CBG); Goroka, Gahavisuka Provincial Park, *Streimann & Kairo* 18184, 18227 (CBG). **Central District.** Mt Wosa, *v. Royen* NGF 20269 (Herb. Aptroot); Mt Albert-Edward, *Kashiwadani* 11747, 11768, 11780, 11809, 11823, 11934, 12001, 12012, 12293 (TNS); 2 km N. of Waiotape Airstrip, *Kashiwadani* 12262 (TNS). **Western Highlands.** Laiagang, Yobobos, *Hoogland & Schodde* 7639b (B). **Milne Bay.** Mt Moiba, *Pullen* 7742 (Herb. Aptroot). **New Ireland:** Hans Meyer Range, *Sands* 1917 (BM). **Solomon Islands: Kolombangara Island.** Ridge west of Kolombangara River, *Hill* 10508, 10537, 10577, 10679, 10603, 10605, 10674 (BM); South Summit, *Hill* 10484–5, 10490 (BM); Poitete, *Glenny* 2280 (BSIP); Irii, *Glenny* 2403 (BSIP). **Guadalcanal Island.** Mt Popomansiu, *Hill* 9286–7, 9330, 9376, 9436, 9443, 9445, 9477, 9478–82, 9482a, 9514–6, 9518, 9567, 9569–70, 9573–4, 9582, 9583–5, 9676, 9678, 9688, 9691, 9696, 9701–3, 9707–8, 9710, 9712, 9719, 9721, 9803, 9829–30, 9835–8, 9857–61 (BM); Mt Gallego, *Hill* 8170 (BM). **Bougainville:** south rim of Lake Loloru crater, 20 miles N. of Buin, *Craven & Schodde* 336 (Herb. Aptroot). **New Caledonia:** *Roberts* (MEL); sine loco, *Compton* 1729 (BM). **New Hebrides: Aneityum.** Sine coll. (BM). **Fiji: Viti Levu.** N-bulti trail, *Selling* (S); Nadarivatu, *O. & I. Degener* 31812e (Herb. Aptroot; B); Mt Victoria, *Green* (BM); *Lam* 6832 (BM); Novai, *Degener* 31815 (B); ridge from Mt Namama to Mt Tomanivi, *Smith* 5712 (US); Ngau, Herald Bay, *Smith* 7828 (US); sine loco, *Horne* (BM); *Milne* (BM). **Samoa: Upolu.** Near Lake Lanoto'o, *Schultz-Motel* 3309 (B); Mt Lanuto'o, *Rechinger* (B, W); Mt Fiamoe,

Schultz-Motel 4251 (B); Viti Savai, *Graeffe* (BM); sine loco, *Powell* (BM). Savai'i. *Reinecke* (WU); ?Tutuila, *Reinecke* (WU).

29. *Pseudocypbellaria trichophora* (Vain.) D.J. Galloway, **comb. nov.**

Fig. 36.

Basionym: *Sticta trichophora* Vain. in *Philipp. J. Sci. Sect. C, Bot.* **8**: 123 (1913). Type: Philippines. Mindanao, Camp Keithley, Lake Lanao, September–October 1907, *Mary Strong Clemens* 1304 (US-isotype).

Thallus orbicular to irregularly spreading, 10–12(–15) cm

diam., loosely to closely attached centrally, free and \pm ascending at margins and apices. *Lobes* linear-elongate (3–)5–8(–12) mm wide, 2–6(–8) cm long, attenuating at apices which may be blunt, rounded or shallowly furcate, \pm dichotomously branching, sinuses prominent, thickened. *Margins* entire, conspicuously thickened-ridged above and below, with prominent white pseudocypbellae, tomentose, especially at or near apices, tomentum white, silky. *Upper surface* dark leaden grey or grey-blue, suffused brownish at margins when wet, pale greyish fawn when dry, tough, coriaceous, smooth or minutely and shallowly wrinkled in parts, plane to \pm canaliculate, isidia, phyllidia and soredia absent. *Pseudocypbellae* present, minute, 0.1 mm diam. or



Fig. 36 *Pseudocypbellaria trichophora*. Isotype (US). Scale in mm.

less, white, punctiform, very widely scattered, inapparent. *Medulla* white. *Photobiont* cyanobacterial. *Lower surface* uniformly thickly tomentose from margins to centre, tomentum dense, woolly-entangled, pale fawnish buff at margins to dark brown or blackened centrally. *Pseudocyphellae* white, prominent (especially at lobe margins), rounded, 0.1–1 mm diam., conical verruciform, margins raised, sharply defined, glossy, decorticate area flat to concave.

Pycnidia not seen.

Apothecia very rare, marginal or submarginal, rounded, cupuliform to 2.5 mm diam., sessile, constricted at base, exciple coarsely wrinkled-scabrid, pale buff-brown, translucent when wet, with white silky hairs prominent below, disc concave to plane, smooth, shining, red-brown, epruinose. *Epithecium* red-brown, 14–20 µm thick. *Hymenium* pale straw or colourless, 90–110 µm tall. *Ascospores* pale red-brown, 1–3-septate, ellipsoid, apices rounded or pointed, 18–25 × 7–11 µm (Vainio (1913: 122) gives spore dimensions as 44–50 × 4–6 µm).

CHEMISTRY. 7β-acetoxypopane-22-ol, hopane-7β, 22-diol (tr.), hopane-15α, 22-diol.

OBSERVATIONS. *Pseudocyphellaria trichophora* has linear-elongate lobes and a coriaceous upper surface which is ± canaliculate towards margins and apices and is devoid of isidia, phyllidia and soredia, but which has rather sparse, white punctiform pseudocyphellae. It has a white medulla, a cyanobacterial photobiont, tomentose lobe margins (especially at apices), a densely tomentose lower surface with conspicuous white pseudocyphellae with raised, narrow margins resembling true cyphellae. It has a two-hopane chemistry. It is distinguished from *P. semilanata* by the tomentose lobe margins and the nature of the pseudocyphellae, and from the New Zealand endemic *P. allanii* (Galloway, 1988) by the scattered pseudocyphellae on the upper surface.

DISTRIBUTION AND ECOLOGY. At present known only from the Philippines and Papua New Guinea. Still very much under-collected. From humid montane rainforest at 1500 m.

ADDITIONAL SPECIMEN EXAMINED. **Papua New Guinea: Morobe.** Aiuwa-Bakia Track, *Streimann & Tamba* 12290 (CBG).

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Morphology and ecology of seedlings, fruits and seeds of Panama: Bixaceae and Cochlospermaceae

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CONTENTS

Introduction	161
Methods	161
Bixaceae	162
Cochlospermaceae	166
Discussion	169
References	171

SYNOPSIS. Seedlings, saplings, fruits and seeds of *Bixa urucurana* (Bixaceae) and *Cochlospermum vitifolium* (Cochlospermaceae) are described, and ecological data on these stages summarized, as part of the ongoing *Seedling Flora Project*, centred on Barro Colorado Island, Panama. Data from these taxa and new seedling characters are used to discuss the relationship between the two families. The presence of extra-floral nectaries at leaf nodes along the stem and 'pearl bodies' on leaves, two ecologically important characters not described in standard floras, are discussed.

INTRODUCTION

The aim of the *Seedling Flora Project*, initiated in 1985, is to produce an illustrated flora of seedlings, saplings, fruits and seeds for the neotropical forest centred on Barro Colorado Island, Panama (see Garwood & Humphries, 1993). In this account, two species are described, *Bixa urucurana* Willd. (Bixaceae) and *Cochlospermum vitifolium* (Willd.) Spreng. (Cochlospermaceae), which are rare on Barro Colorado Island (BCI) but common in other parts of central Panama. Although the two families are treated separately in the *Flora of Barro Colorado Island* (Croat, 1978), *Flora of Panama* (Robyns, 1967a, b; D'Arcy, 1987), and the *Flora neotropica* (Poppendieck, 1981), they are closely allied and often combined into one family, the Bixaceae (Corner, 1976; Cronquist, 1981).

METHODS

Seeds were collected in central Panama, and sown while fresh under sun and shade conditions in a screened growing house on Barro Colorado Island. Seedlings were photographed, observed for fresh characters, and harvested at irregular intervals; several individuals were grown to sapling size. Each seed collection has a unique collection number: voucher specimens and the seedlings grown from that collection are lettered sequentially according to date of collection or har-

vest, e.g. 1784A (adult voucher), 1784B-G (seedlings). Adult voucher specimens are deposited among the following herbaria: F, BM and PMA. All seedling, fruit and seed specimens described are currently at BM, where seedling voucher specimens and fruit and seed samples will be deposited; duplicates of seedlings will be distributed to other herbaria.

Descriptions are based on photographs and notes of fresh specimens and on dry and preserved material from the collections described above, supplemented with general information from published floras. Taxonomic references used throughout the descriptive parts are summarized after the notes on family habit and distribution; references are cited in the fruit and seed descriptions only when they are the sole source of specific information; those used in the ecology section are cited in the text.

For each species, information is stored in a detailed database and output in a standard format that will be used for all 700 species in the *Seedling Flora Project*. Descriptive terms are being standardized across all families, but generally follow common usage. See de Vogel (1980) for definitions of seedling-specific terms. The following less conventional terms are used: length of pubescence or size of other surface features, minute (< 0.1 mm), short (0.1–0.5 mm), long (0.5–1.0 mm), very long (> 1.0 mm). Leaf nodes are numbered sequentially from the first leaf-bearing node above the cotyledons. A more detailed account of seed germination for all species is being prepared (Garwood, in prep.). In this account, the median time until germination is given, rather than the mean, because the distribution of germination time is highly skewed.

BIXACEAE

HABIT AND DISTRIBUTION. Shrubs or trees. Neotropical, but the cultivated *Bixa orellana* L. is planted throughout the tropics; one genus and five species, two species in Panama and one or two species known from BCI (see below).

TAXONOMIC REFERENCES. Macbride (1941), Standley & Williams (1961), Robyns (1967a), Dathan & Singh (1972), Baer (1976), Corner (1976), Croat (1978), Molau (1983).

Bixa L.

TAXONOMIC NOTES. Five species of *Bixa* are present and distinct in the Amazon basin (Macbride, 1941; Baer, 1976; Molau, 1983), including the widely cultivated *B. orellana* L. sensu stricto and its cultivars. Typical examples of *B. urucurana* Willd. and *B. orellana* L. occur throughout Central America, but intermediate forms have been reported (Baer, 1976) and Central American floras have combined the two taxa or ranked them as varieties of *B. orellana* L. sensu lato (Standley & Williams, 1961; Robyns, 1967a). See Dempsey & Garwood (1994) for further discussion of these two taxa.

The BCI taxon, described as *B. orellana* L. by Croat (1978), is probably *B. urucurana* Willd. Its distribution along the shoreline of BCI (Croat, 1978), where lake levels fluctuate greatly throughout the year, is consistent with the habitat of *B. urucurana* but not *B. orellana*. *B. urucurana* is usually found along stream and river banks and in seasonally inundated or periodically brackish low areas, whereas *B. orellana* does not tolerate waterlogged soils (Baer, 1976). In addition, the only *Bixa* seedlings I have encountered on BCI (Garwood 2439) were growing on a sandy beach at the mouth of a small stream. One BCI specimen (Croat 12294) has been identified as *B. urucurana* (Baer, 1976), but I have not verified others listed in Robyns (1967a) and Croat (1978). However, it would be surprising if the commonly cultivated *B. orellana* has never been planted on BCI, as many ornamental and food plants have been cultivated in the laboratory clearing and older settlement sites.

Bixa urucurana Willd., *Enum. pl.*: 565 (1809).

Fig. 1.

HABIT AND DISTRIBUTION. Small tree, to 10 m tall, of moist to wet lowland forest, usually along streams, rivers or other inundated areas. Brazil and Peru to Nicaragua or Guatemala.

COLLECTIONS. **Panama.** Colón: Gamboa, along shoreline of Rio Chagres, Garwood 1830A (BM, F, PMA, adult vouchers), Garwood & Rand 2085A (no voucher, same tree as Garwood 1830A); Barro Colorado Island: shoreline, Garwood 2439 (seedlings); 7 seedlings to 69 cm tall examined (Garwood 1830B–D, 2085B–C, & 2439).

Fruits

Infructescences terminal; loosely branched panicle-like thyrse to about 22 cm long, with 1–3 fruits usually maturing per branch. Rachis to about 22 cm long; branches to about 5 cm long; pedicels 1.5–2.0 cm long with 5 large glands about 2.5 mm tall below calyx scars; all stems densely scaly. **Receptacles** undeveloped. **Stipes** to 1 mm long, straight, circular in t.s., scaly, remaining attached to capsule. **Fruits** capsules, dry

(with slightly fleshy seeds); from superior ovaries, with corolla and sepal scars inconspicuous among 5 large, extrafloral glands at base; carpels 2; locules 1. Capsules papery to woody, indehiscent or tardily loculicidally dehiscent; partially septate; 15–30(45) × 15–30 × 10–25 mm, (including spines); straight; circular to transversely elliptic in outline, circular in t.s.; margins entire; base widely rounded to truncate; apex widely rounded to truncate, with a terminal cluster of tightly packed short spines; densely covered with large, stiff spines, to 5 mm tall, with enlarged bases usually touching; surface medium to dark brown to red-brown, dull, with short weak spines < 0.5 mm tall among bases of larger spines; sparsely to moderately scaly, especially around bases of larger spines; scales peltate, orange-brown to brown, ± sessile to stalked. Seeds 6–12, central, touching along 1–2 sides, slightly deformed by neighbours; long axis of seed oblique to central axis of fruit. **Placentae** parietal; each a 2 mm wide dark band on lower half of endocarp, with seeds in 2 rows, and dark band narrowing above seeds and continuing to apex. **Funicle** about 2 mm long, curved to coiled, cylindrical, persistent on placentae, flared apically into shiny, 2-lobed appendage below seed, 1.5–2 mm long, each lobe a series of undulating compressed folds. **Septa** marginal, extending full-length of fruit but < ¼ distance to centre, about 2 mm tall throughout its length, solid basally but perforated apically, located under placenta but hidden by endocarp. **Valves** 2, dehiscent from apex if tardily dehiscent, spreading apart slightly, remaining attached at base. **Fruit wall** thin, about 0.5 mm wide (excluding larger spines), 3-layered, endocarp separating from outer fruit wall at maturity. **Exocarp** very thin, about 0.05 mm wide, ± crustaceous, dark brown. **Mesocarp** thin, about 0.25 mm wide, forming most of septa, ± cartilaginous from numerous reticulate, tough fibres, which continue into bases of larger spines; spaces between fibres filled by ± papery matrix, which is compressed, shiny and mottled with orange-brown on inner surface, medium brown with cream-coloured fibres. **Endocarp** very thin, ≤ 0.05 mm wide, dry-membranous, dark brown to orange-brown; inner surface rough, glabrous, dull, dark brown to orange-brown.

Seeds

Seeds 3.7–5.1 × 3.5–4.3 × 3.0–3.8 mm; sarcotestal; anatropous; widely obovate or widely obtriangular in outline, compressed except subcompressed apically, mostly ± elliptic in t.s., with both faces often concave; margins entire; base moderately acute; apex truncate; apical cap over chalazal foramen moderately raised, circular, ≈ 2 mm wide, with light brown outer ring and black centre, both easily dislodged; deep medial groove extending > ¾ length of seed, from hilum to apex along raphe; outer surface densely pustulate when dry, papillate when moistened, rough between pustules at higher magnification, glabrous, slightly glossy when dry, medium orange-brown or red-brown when dry, papillae yellow when moistened; if sarcotesta eaten or removed, then outer surface smooth, smooth at higher magnification, glabrous, glossy, medium brown to orange-brown, except dark black-brown at base around micropylar regions. **Aril** absent. The funicular appendage (see above), which Corner (1976) describes as a vestigial aril, remains firmly attached to the funicle. **Sarcotesta** hard when dry, fleshy when moistened; with large oil cells resin-like when dry, becoming soft and waxy when moistened, but drying firm and waxy; completely surrounding seed; initially medium brown to orange-brown

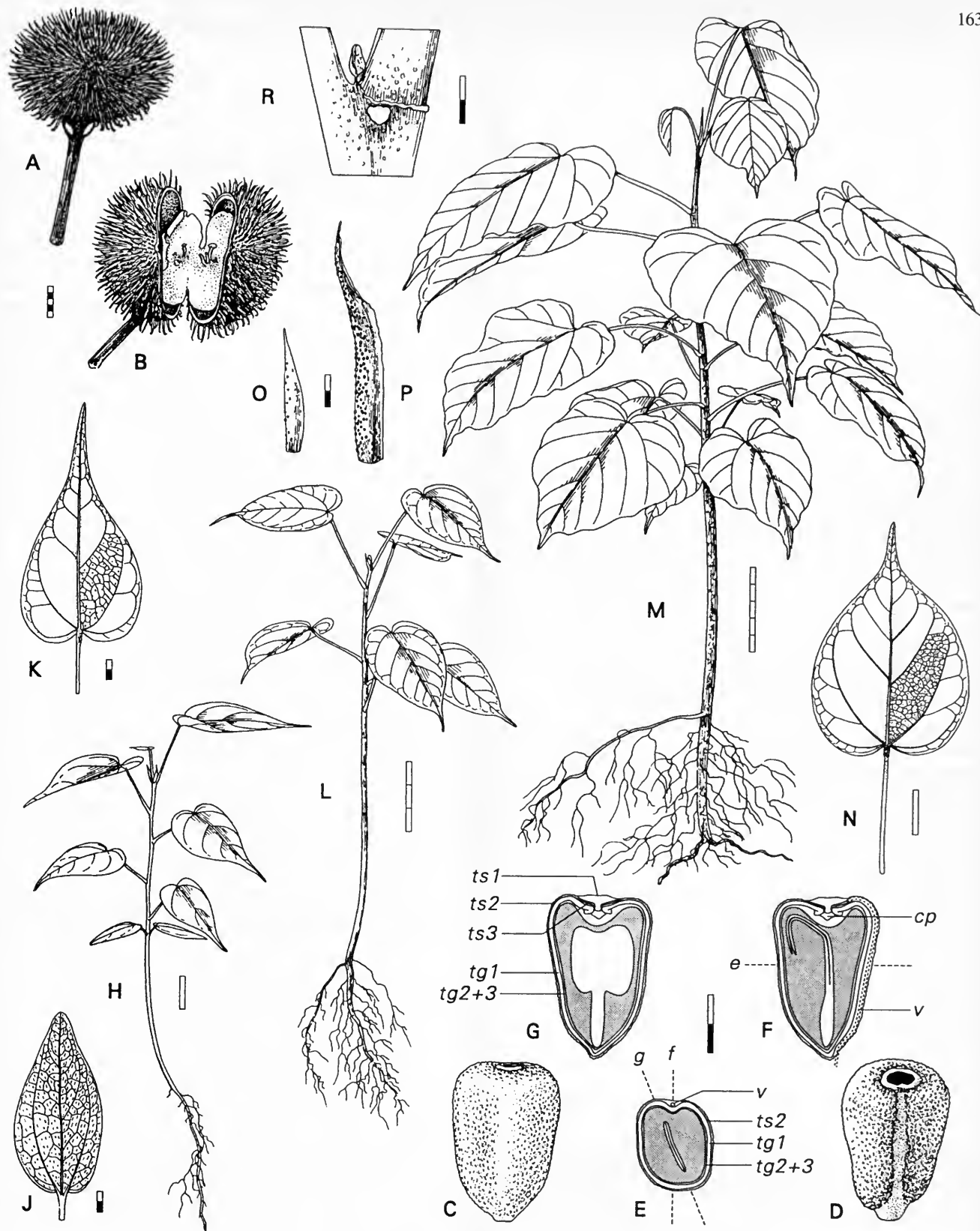


Fig. 1 *Bixa urucurana* Willd. Fruit: A, indehiscent capsule; B, forcefully opened capsule. Seed: C-D, two views; E, t.s. (through plane 'e' in F); F, medial l.s. (through plane 'f' in E); G, oblique l.s. (through plane 'g' in E). Seedling: H, older seedling; J, cotyledon; K, first leaf. Saplings: L, young sapling; M, older sapling; N, leaf at about node 17; O, stipule at about node 24; P, stipule at about node 45; R, gland at about node 40. Scale bars: black and white, 1 mm units; white only, 1 cm units. Symbols: outer to inner layers of testa (ts1-ts3) and tegmen (tg1-tg3); vascular trace (v); chalazal plug (cp); endosperm (shaded); and cross-sectional planes for E, F, and G (dashed lines: e, f and g, respectively).

when dry, becoming yellow or orange-yellow when moistened (and remaining so upon redrying); initially \pm pusticulate when dry, becoming \pm papillate when moistened (and remaining so); developing from entire testa. *Hilum* subbasal in medial groove, exposed, slightly recessed to flush, sometimes raised around end of vascular bundle, medium orange-brown, slightly lighter than surrounding sarcotesta, black-brown if tegmen exposed, usually indistinct and ill-defined, sometimes distinct, elliptic and \approx 1 mm long when much of sarcotesta adheres to funicle, often with irregular patch of tegmen exposed over the micropylar region. *Micropyle* basal, not visible. *Chalazal foramen* apical, not visible until apical cap removed, conspicuous on tegmen, round, \approx 1.25 mm wide; closed by black chalazal plug, flat-topped, \pm shallowly conical, \approx 0.5 mm wide, on a brown, \approx 1.5 mm wide disk, an extremely complex structure formed from specialized chalazal tissue (hypostase) and tegmen. *Endosperm* thick, encasing embryo, hard, rapidly becoming soft once moistened, starchy (Corner, 1976), cream-coloured to white. *Embryo* large, to 5 mm long, central, with cotyledons in plane oblique to medial plane through raphe, straight except abruptly curved at apex of cotyledon under chalazal plug, spatulate, flattened, yellow or yellow-green; axis well-developed, completely exposed; cotyledons well-developed, flat, often slightly curved, thin, ovate in outline, cordate at base; plumule rudimentary. *Vascular bundle* lateral, unbranched, very thin, sometimes exposed at hilar end, passing through sarcotesta in the medial groove of the raphe, sometimes visible through sarcotesta, terminating apically in chalazal cap. *Seed coat* thick, mostly 0.125–0.25 mm wide, except to 1.0 mm wide over chalaza, bony, with fleshy sarcotesta, exotegmic. *Testa* thin when dry, thicker in medial groove, \pm thick when moistened, resin-like when dry, a fleshy sarcotesta when moistened, mostly 1-layered except 3-layered at apex around chalazal foramen; outer layer very thin, crustaceous, only evident as apical cap over chalazal foramen, light brown with black centre; middle layer (see sarcotesta above) less developed beneath apical cap; inner layer thick, bony, dark-brown, only evident below apical cap, tightly appressed to tegmen and lining the chalazal foramen. *Tegmen* thick, bony, quickly becoming leathery during imbibition, impermeable on outer surface but highly permeable on inner surface, 3-layered; outer layer thick, \pm bony, cream-coloured to light grey, inflexed apically forming chalazal foramen, with a very thin dark brown inner band that becomes thick at base around micropylar area and forms a thick dark internal ring around chalazal foramen; middle layer very thin, \pm papery, light brown, except thick and spongy around chalazal plug, splitting during imbibition and partially adhering to outer and inner layers; inner layer very thin, \pm papery, medium brown, except \pm thick, bony and black-brown beneath chalazal plug, separating from middle layer during imbibition, becoming leathery (except under chalaza), and adhering to endosperm.

Seedlings and saplings

Seedlings phanero-epigeal with cotyledons haustorial during germination, then photosynthetic.

DEVELOPMENT. Hypocotyl elongates into loop, the cotyledons emerge from seed, sometimes not fully escaping seed. Hypocotyl straightens.

ROOTS. *Primary root* circular in t.s., curved to sinuous, light

brown; surface texture and colour between hypocotyl and root change slightly and gradually around collet. *Secondary roots* sinuous, scattered along primary root. *Root hairs* not evident. *Sapling root system:* taproot long-tapering, very thick for much of length; secondary roots mostly very thin and common, a few moderate-sized; rootlets very fine to fine and numerous.

STEMS. *Hypocotyl* 34–38 \times 1–2 mm, circular in t.s.; smooth, drying longitudinally wrinkled; glabrous; green. *Epicotyl* 1–5 \times 0.5–2 mm, circular in t.s., smooth, sparsely minutely scaly, green. Scales peltate, \pm sessile, erect, light orange-brown. *Cataphylls* absent. *Internodes* 1–10, 3–17 mm long; later internodes to 40 mm; circular in t.s.; smooth; glands absent on internodes 1–10, present below the stipule scar and well-developed on most internodes \geq 20, secreting nectar 3–4 internodes below youngest leaf, to 1 mm tall, widely obovate, with apex rounded to obcordate, light brown-green when fresh, drying light brown on glabrous raised pad twice width of gland and darker brown than surrounding stem; sparsely scaly at internodes 1–5, moderately scaly through internode 20, densely scaly at later internodes; slightly pusticulate at early internodes, often moderately to densely pusticulate at later internodes, pustules often still filled with dark orange-brown fluid on dry specimens. Scales peltate, \pm sessile, light orange-brown, \approx 0.05 mm in diameter at first internode to 0.10 mm in diameter at later internodes, \pm circular with entire to irregular margins. *Older stems* dark brown-green to dark grey-brown, solid basally, often hollow apically, shallowly furrowed, rough and often glabrous with age as initial bark surface fragments; wood cream-coloured. *Lenticels* first appearing on older stems \approx 2–5 mm wide, common on older stems 6–8 mm wide; mostly \approx 0.5 mm long, raised, initially elliptic to round, widening with age, cream-coloured on darker stems. *Buds:* Cotyledonary buds hidden or slightly protruding to 0.2 mm out of axils, slightly protruding above cotyledon scars, glabrous. Lateral buds protruding \approx 0.2 mm out of axils at early nodes, to 1 mm at later nodes; glabrous at early nodes to moderately or densely scaly at later nodes; enclosed within at least 2 widely to very widely triangular scale leaves. Terminal buds covered by stipules, glabrous at nodes 1–10, gradually becoming densely scaly at later nodes.

COTYLEDONS. Two, opposite, foliaceous, simple, petiolate, estipulate, emergent from seed, spreading apart, persistent until at least node 5 matures. Blades 15–18 \times 8–10 mm; straight, flat, ovate; apex acute to narrowly rounded; base \pm cordate; margins entire. Blades densely thick-lined below, each to 0.5 mm long, parallel to long axis of cotyledon, light brown-orange, faintly pellucid and yellow-brown against strong light; faintly pellucid thick-lined above against strong light, otherwise scarcely visible; glabrous above and below; green. *Venation* palmate, 3-veined; brochido-actinodromous, basal and perfect. Primary veins 3; fine to moderate-sized; moderately raised above when dry, prominently raised below; central primary vein moderate-sized, straight to sinuous apically; lateral primary veins basal, fine, $>$ $\frac{3}{4}$ length of blade, curved or slightly arched, diverging at narrowly acute angles, looped, obtusely to perpendicularly joined to secondaries of midvein. Secondary veins fine; 10–18 per cotyledon, 4–5 along midvein and 3–4 along each lateral primary vein; alternate along midvein, marginal along lateral primary veins; \leq $\frac{1}{2}$ length of blade, longest centrally along midvein; arched; diverging at mostly narrowly acute angles; looped,

variously joined to superadjacent secondaries; slightly raised above, slightly raised to flush below. Inter-secondary veins occasional. Tertiary veins reticulate within intercostal area, looped within marginal area. *Petioles* 2–3 mm long, half-circular in t.s., channelled, often warty along margins and at apex above.

LEAVES. Alternate and spiral; simple; long-petiolate, stipulate. Leaf blades 22–25 × 12–13 mm at first node; 25–40 × 14–20 mm at nodes 2–5; to 229 × 168 mm at later nodes; straight; ovate at nodes 1–5, becoming widely ovate at later nodes; apex long-acuminate at nodes 1–5, becoming acuminate or short-acuminate at later nodes; base cordate at nodes 1–20, usually becoming emarginate, truncate or widely rounded at later nodes; margins entire. Blades dark green above, lighter below; raised between the veins when fresh; papery; usually densely minutely light orange-brown or green-brown punctate on blade below at early nodes, becoming dark brown punctate at later nodes, sometimes with thick dark brown-orange lines on veins below at later nodes, each punctation usually 0.05–0.10 mm long, irregular, circular or ± elliptic in outline, usually yellow-green pellucid against strong light at early nodes to light orange-brown pellucid at later nodes, sometimes opaque and dark brown-orange at later nodes, often associated with short thin or thick pellucid canals, sometimes branched; sometimes moderately punctate above, but usually pellucid dots scarcely visible above except against strong light; glabrous to sparsely minutely scaly below on veins and blades at nodes 1–5, becoming moderately scaly at later nodes; glabrous to sparsely minutely scaly above on veins and blades at nodes 1–5, becoming mostly sparsely scaly at later nodes; glabrous along margin. Scales peltate, ± sessile, light orange-brown, mostly ≤ 0.05 mm in diameter on blade, to 0.10 mm on veins below, ± circular with entire to irregular margins. *Young leaves* spreading open almost immediately, glabrous or sparsely scaly below at early nodes to densely scaly below at later nodes; initially densely pustulate above, with shiny coating above apparently secreted by pustules when leaf about $\frac{1}{4}$ – $\frac{3}{4}$ expanded, surface becoming ± dull again when full-size, dark green-brown, becoming dark brown-green, rigid, descending, produced continually, often before previous 1–3 leaves full-size. *Venation* palmate, 5-veined; brochido-actinodromous, basal, perfect. Primary veins 5; moderate-sized; moderately raised above, prominently raised below; central primary vein straight; lateral primary veins basal, thinner than midvein, inner pair of lateral primaries $\frac{1}{2}$ – $\frac{3}{4}$ length of blade, arched, diverging at moderately acute angles, looped, acutely to perpendicularly joined to secondary vein from midvein; outer pair < $\frac{1}{2}$ length of blade, arched, diverging at ± perpendicular angles, looped to diffusely looped, perpendicularly to obtusely joined to secondary vein from inner lateral primary vein. Secondary veins moderate-sized along midvein, fine along lateral veins; 4–6 along midvein and 2–3 along each inner lateral vein on leaves at first node, 4–8 along midvein and 2–4 along each inner lateral vein at nodes 2–5, 8–15 along midvein and 2–8 along each inner lateral vein at nodes ≥ 12; alternate to subopposite along midvein, on outer (exmedial) side of lateral veins; ≤ $\frac{1}{3}$ length of blade, longest centrally along midvein; mostly arched, often hooked apically along midvein and distally along lateral primary veins; diverging at moderately acute angles; looped, sometimes diffusely looped centrally along lateral primary veins, mostly perpendicularly joined to superadjacent secondary vein; slightly raised above,

moderately raised below. Inter-secondary veins absent to occasional in intercostal areas along midvein. Tertiary veins looped within marginal area, ± reticulate within intercostal area at nodes 1–5, becoming straight-percurrent and oblique to midvein near margin and convex-percurrent near midvein at later nodes. *Petioles* 10–140 mm long, 10–20 mm long at nodes 1–5; straight, circular in t.s.; often drying channelled above, enlarged at base, pulvinate at apex, medium yellow-green to green with medium brown pulvinus; sparsely to moderately pustulate, sparsely minutely scaly at early nodes becoming moderately scaly at later nodes, pulvini usually densely pustulate and densely scaly at later nodes. *Stipules* paired; 2–5 mm long at nodes 1–5, to 19 mm long at later nodes; simple, narrowly triangular, with long acuminate apex; quickly deciduous, papery; glabrous at early nodes to densely scaly at later nodes; green becoming light-brown; leaving pair of conspicuous scars above petiole, perpendicular to stem, each > $\frac{3}{4}$ width of stem.

SAP. Not evident in freshly cut leaves, bark, or roots, but slowly oozing out around central pith of cut stem, drying cream-coloured to medium orange-brown and resin-like.

ODOUR. Not distinctive.

ARCHITECTURE. Trunk axis monopodial. Initial axis orthotropic. No branches formed on plants ≤ 70 cm tall, but elongated lateral buds (to 4 mm long) on largest individual suggest that sylleptic branches might soon be produced. Leaves held ± horizontal to descending.

Ecology

PHENOLOGY. Central American *B. urucurana* flowers in the late rainy season September–December, with fruit developing during the following dry season. Fruits from my Panamanian collections were dark brown and dry in April and May.

DISPERSAL. When ripe, the dry capsule is dark brown with stiff spines, and probably indehiscent (Baer, 1976) or at most tardily dehiscent. Seeds within the dry, indehiscent fruit are also dry and dark orange-brown to red-brown, but the sarcotesta becomes soft, papillate and bright yellow when moistened. Dispersal mode is unknown. Seeds of the genus *Bixa* are usually assumed to be bird-dispersed because of the bright red or red-orange sarcotesta visible in the dehiscent capsule, but Baer (1976) notes there are no observations of birds taking the seeds. In the indehiscent fruits of *B. urucurana*, the duller orange-brown to red-brown seeds are not visible at maturity and are unlikely to attract birds. Given its riverside habitat, suggestions of fish-dispersal (van Roosmalen, 1985) or water-dispersal (Baer, 1976) are not unreasonable. In addition, the spiny, dry, brown indehiscent fruits hiding pulp-covered seeds are reminiscent of *Apeiba membranacea* Spruce ex Benth. (Tiliaceae), which is mammal-dispersed.

GERMINATION. Seeds of *B. urucurana* germinated slowly (22–38 weeks) at low percentages (5–12%) in both sun and shade in the growing house. Baer (1976) failed to germinate seeds of numerous samples of *B. urucurana*, although those from *B. orellana* sensu stricto germinated easily. Seeds collected from unopened fruit of the cultivated *B. orellana* sensu stricto have high moisture content (≈ 45%, fresh weight basis [FWB]) and permeable seed coats (Goldbach, 1979), and germinate rapidly (< 1–3 weeks; Garrard, 1955; Goldbach,

1979; Chin et al., 1984). When seeds are air-dried, they become impermeable, moisture content drops ($\leq 10\%$ FWB), and germination becomes sporadic over > 1 year. Under natural conditions, the chalazal plug must become loosened before imbibition and germination can occur, but this requirement can be circumvented if seeds are scarified by cutting off the micropylar tip of the seed coat below the radicle (Goldbach, 1979). The proportion of impermeable seeds in a collection varies from 0% (Garrard, 1955) to $> 50\%$ (Goldbach, 1979), depending on seed moisture content, period of drying, and possibly cultivar used. My collections of *B. urucurana* had low seed moisture contents (6–10%, FWB), suggesting that the seed coats were impermeable at time of dispersal. Seeds of *B. orellana* air-dried to about 10% moisture content (FWB) and stored for 12 months in the laboratory at 23°C retained high viability (95% of initial viability); those dried to about 4% moisture content had slightly lower viability (82% of initial values) over the same period (Goldbach, 1979). Baer (1976) also reports high viability after 1 year, whereas Garrard (1955) found viability was completely lost after 5 months. The latter may reflect the absence of seeds with impermeable coats in that collection.

COCHLOSPERMACEAE

HABIT AND DISTRIBUTION. Trees, shrubs, subshrubs or rhizomatous herbs. Tropical; two genera and 15 species, one genus and two species in Panama, and one species known from BCI.

TAXONOMIC REFERENCES. Robyns, (1967b), Dathan & Singh (1972), Corner (1976), Croat (1978), Poppendieck (1980, 1981).

Cochlospermum Kunth

HABIT AND DISTRIBUTION. Small trees, shrubs, or subshrubs. Pantropical, mostly South American; 12 species, two species in Panama, one species known from BCI.

***Cochlospermum vitifolium* (Willd.) Spreng., Syst. 4(2): 406 (1827).**

Fig. 2.

HABIT AND DISTRIBUTION. Small sparsely branched trees, 3–12 m tall, of dry to moist lowland forests or savannas, common in young secondary forest, and along frequently burned roadsides. Mexico to Bolivia, northern Brazil and West Indies; introduced into Paletropics.

COLLECTIONS. **Panama.** Colón: Gamboa, beginning of Pipeline Road, Garwood & Lighton 1784A (F, PMA, adult vouchers); same locality, Garwood 2941A (BM, fruit voucher); Barro Colorado Island: Garwood 3060A (BM, seed voucher); 20 seedlings to 81 cm tall examined (Garwood 1784B–G, 2941B, 3060B).

Fruits

Infructescences terminal; sparsely branched panicle-like thyrses, with 1(–2) fruit maturing per branch, capsules suberect to pendent. Stems woody, glabrous or pubescent; peduncles 2–5 cm long, rachis and branches about 3–20 cm

long, pedicels 3–4 cm long. **Receptacles** undeveloped. **Stipes** absent. **Fruits** capsules, dry; from superior ovaries, with withered persistent sepals, to 28 mm long at base; carpels 5; locules 1. Capsules papery to woody, locucially and septicidally dehiscent (outer and inner valves, respectively); partially 5-septate; (40–)70–90(–110) \times 35–70 \times 35–70 mm; straight; obovate or widely ovate or elliptic in outline, circular in t.s.; margins entire; base truncate to short-attenuate; apex truncate and centrally depressed; surface dark brown or grey, dull, densely longitudinally narrowly multi-ridged, moderately to densely minute- to short-pubescent; hairs simple, erect. Seeds numerous, intermediary, touching along compacted cotton-like hairs but seed bodies separate, compressed \pm laterally; long axis of seed parallel or oblique to long axis of fruit; at maturity, free within locule. **Placentae** intruded parietal; each cylindrical, running \pm full length of fruit, ≈ 50 –60 \times 5–6 mm, with numerous large funicular mounds, minute ovule scars, and aborted ovules and seeds. **Funicle** to 0.5 mm tall, straight, widely to very widely conical, persistent on placentae. **Septa** marginal, extending $\frac{1}{2}$ – $\frac{3}{4}$ distance to centre. **Valves** 10, 5 outer and 5 inner, dehiscent from apex, spreading apart, each outer valve overlapping margins of adjacent inner valves except open at apex, outer valves remaining attached at base or by thread-like extension of placentae or sometimes falling; inner valves eventually falling out. **Fruit wall** thin, about 1.0 mm wide, 3-layered, endocarp separating from outer fruit wall at maturity. **Exocarp** thin, \pm woody, with tough closely spaced longitudinal fibres, dark brown or grey. **Mesocarp** thin on inner surface of outer valves, forming thin septa and thickened placentae, spongy to cobwebby, with conspicuous vascular fibres transverse to oblique and sinuous on valves and oblique and often branched on septa, cream to light brown. **Endocarp** very thin, forming 5 separate elliptic inner valves, dry-membranous, translucent, dull, light brown or orange-brown; inner surface with central longitudinal ridge and numerous \pm reticulate ridges, glabrous, glossy. When fruit unripe, exocarp green.

Seeds

Seeds 4–5 \times 3–4 \times 1–2 mm; campylo-anatropous (Corner, 1976); C-shaped in outline, sometimes slightly coiled, circular in t.s.; margins entire; base eccentrically short-attenuate; apex rounded; outer surface rough except wrinkled in sinus, densely very long-pubescent except glabrous in sinus, with hairs to 14 mm long, erect, sinuous, white, fluffy and cotton-like, easily detached after dispersal; dull, mostly medium brown except red-brown or orange-brown or dark brown in sinus; exfoliating to reveal tegmen, then base rounded, outer surface smooth, minutely cellular at higher magnification, glabrous, glossy, black. **Aril** absent. **Sarcotesta** absent. **Hilum** basal and eccentric to subbasal, toward sinus, exposed, prominently raised on testa, not visible on tegmen after testa exfoliates, cream-coloured, lighter than testa, circular. **Micropyle** basal, centric, exposed but partially hidden by hilar mound, prominently raised on testa, only slightly raised on tegmen, \pm conical to cylindrical on testa, punctiform on tegmen. **Chalazal foramen** subapical in sinus, not visible on testa but conspicuous on tegmen, round, about 0.6 mm wide; filled by black chalazal plug, conical on 0.8 mm wide disk, similar in composition to tegmen. **Endosperm** thick, encasing embryo, \pm hard, oily (Cronquist, 1981), white. **Embryo** moderate-sized, ≈ 4 –6 mm long, central, C-curved, \pm spatulate when straightened, compressed; axis moderately

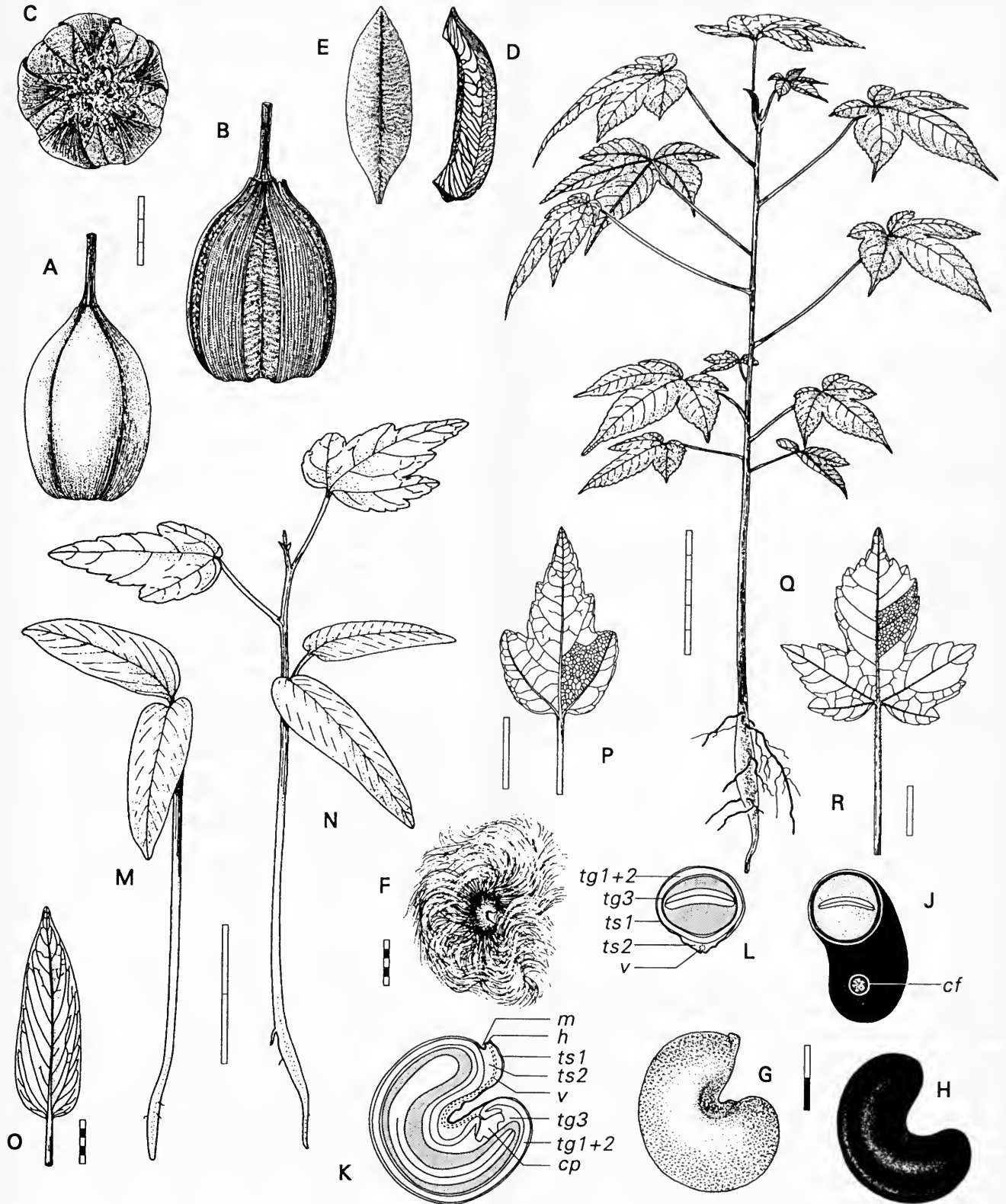


Fig. 2 *Cochlospermum vitifolium* (Willd.) Spreng. Fruit: A, green, undehiscent capsule; B, dehiscent capsule, side view; C, dehiscent capsule, apical view; D, outer valve, with placenta; E, inner valve. Seed: F, complete seed with testal hairs; G, hairs removed to show surface of testa; H, testa removed to show surface of tegmen; J, partial seed, testa removed to show chalazal foramen in sinus; K, l.s. of seed without hairs; L, t.s. through sinus. Seedling: M, young seedling; N, older seedling; O, cotyledon; P, first leaf. Sapling: Q, sapling; R, leaf at node 4. Scale bars: black and white, 1 mm units; white only, 1 cm units. Symbols: outer to inner layers of testa (*ts1*–*ts2*) and tegmen (*tg1*–*tg3*); vascular trace (*v*); hilum (*h*); micropyle (*m*); chalazal plug and foramen (*cp* and *cf*); and endosperm (shaded).

developed, exposed; cotyledons moderately developed, flat, thin, entire; plumule rudimentary. *Vascular bundle* lateral in sinus, unbranched, thin, exfoliating with testa; passing through raphe, terminating subapically in chalazal foramen. *Seed coat* very thick, bony, exotegmic. *Testa* very thin, \pm thicker in sinus, crustaceous, loosely surrounding tegmen, often exfoliating, 2-layered except 3-layered in sinus; outer layer thin, \pm crustaceous, light brown except red-brown or orange-brown in sinus, densely long-pubescent (see above); middle layer absent except \pm thick in sinus, hard-spongy, cream-coloured; inner layer thin, \pm crustaceous, black. *Tegmen* very thick, \pm bony to glassy, 3-layered; outer layer very thin, waxy, \pm clear; middle layer thick, bony to glassy, \pm 3-banded, with cream then brown then black bands; inner layer thin except thicker under chalazal foramen, cream-coloured, membranous to spongy, with abundant red-brown compressed globules (gum cavities).

Seedlings and saplings

Seedlings phanero-epigeal with cotyledons haustorial during germination, then photosynthetic.

DEVELOPMENT. Radicle emerges from hilar region and slightly elongates, as cotyledons absorb endosperm. Hypocotyl elongates into loop, then straightens, pulling cotyledons from seed. Cotyledons expand, sometimes not fully escaping seed, which is often carried upwards on tip of cotyledons. Cotyledons are usually fully expanded within 2 weeks of germination. Shoot rest period is short during the cotyledon stage, sometimes lasting < 1 week in sun. Shade-grown seedling usually die without advancing past the cotyledonary stage. Growth is continuous in sun, with a new leaf initiated about every 1–2 weeks, often before the previous leaf has reached full-size.

ROOTS. *Primary root* $\approx 30 \times 1$ mm, poorly developed in shade, circular in t.s., straight to sinuous, cream-coloured becoming brown; surface texture and colour between hypocotyl and root change slightly and gradually around collet. *Secondary roots* to 0.2–0.3 mm wide, sinuous, sparsely scattered along primary root. *Root hairs* appear quickly on primary root. *Sapling root system:* taproot with tuberous swelling (xylopodium), to 50×15 mm, forming 10–20 mm below collet, developing in first year, produced on some seedlings only 12 cm tall; taproot long-tapering below swelling, thin to moderate-sized; secondary roots thin to moderate-sized, few to common; rootlets fine, few to common.

STEMS. *Hypocotyl* $33\text{--}71 \times 0.5$ mm, circular in t.s.; slightly grooved apically below petioles; glabrous basally becoming densely minute-pubescent in apical $\frac{1}{2}\text{--}\frac{1}{3}$; medium yellow-green, often medium red-brown in sun. Hairs simple, erect to ascending, curved, clear to cream-coloured. *Epicotyl* $9\text{--}17 \times 0.5$ mm, circular in t.s., densely minute-pubescent, medium yellow-green to dark green. Hairs simple, erect to ascending, curved or sinuous or coiled, clear to cream-coloured. *Cataphylls* absent. *Internodes* 1–10, 2–17 mm long; later internodes to 65 mm; circular in t.s.; densely pubescent on side above petioles but glabrous to sparsely minute-pubescent on other side, glabrous to sparsely pubescent at later nodes, with abundant pearl bodies on youngest internode; medium yellow-green to dark green. Hairs simple, erect to ascending, curved or sinuous or coiled, clear to cream-coloured. Pearl bodies minute, globular, 0.05–0.075 mm in diameter, erect,

short-stalked, clear, usually drying orange-brown. *Older stems* medium grey-green then medium grey-brown, solid with small soft pith basally to hollow apically; wood cream to cream-brown, with \pm white rays, porous. *Lenticels* appearing on stems > 3 mm wide, common on stems > 4 mm; $\leq \frac{1}{2}$ mm long, round, widening with age, slightly raised, dark brown, on lighter stems. *Buds:* Cotyledonary buds hidden in axils, usually inconspicuous above cotyledons scars, rarely protruding on older stems. Lateral buds hidden in axils at early nodes to protruding out of axils at later nodes, glabrous to slightly pubescent, enclosed within at least 2 scale leaves. Terminal buds naked, covered by stipules from several nodes, moderately pubescent.

COTYLEDONS. Two, opposite, foliaceous, simple, petiolate, estipulate, emergent from seed, spreading, persistent until nodes 2–7 mature (usually for 2–4 weeks, sometimes to 13 weeks). Blades $24\text{--}26 \times 7\text{--}8$ mm; straight, flat, narrowly ovate; apex narrowly acute or acute; base obtuse or emarginate or truncate; margins entire. Blades glabrous above and below; green above, lighter below. *Venation* pinnate; eucamptodromous, sometimes brochidodromous in apical third. Midvein fine; straight to slightly sinuous; impressed above except slightly raised apically when dry, moderately raised below. Secondary veins moderate-sized; 16–18; mostly alternate except opposite at 2–4 basal veins; $\frac{1}{3}\text{--}\frac{2}{3}$ length of blade, longest basally; slightly curved; diverging at narrowly acute angles; open, branching and terminating near or at margin; slightly raised to flush above, slightly raised to flush below. Inter-secondary veins occasional. Tertiary veins inconspicuous and reticulate. *Petioles* 4–5 mm long, straight, half-circular in t.s., moderately channelled, mostly glabrous below, densely minute-pubescent above, with abundant pearl bodies above.

LEAVES. Alternate and spiral; simple; long-petiolate, stipulate. Leaf blades $21\text{--}33 \times 13\text{--}22$ mm at first node; $18\text{--}67 \times 12\text{--}70$ mm at nodes 2–10; to 190×210 mm at later nodes; ovate to widely ovate at nodes 1–2, becoming widely ovate to very widely ovate at nodes 3–10, mostly widely ovate to depressed ovate at later nodes; unlobed to palmately 3-lobed or 3-cleft at first node, becoming 3-parted, with central lobe largest and 2 large basal teeth becoming increasingly lobe-like at nodes 2–20, often 5-parted at later nodes, with central lobe at least slightly larger; apex of lobes mostly acute or acuminate at nodes 1–10, often long-acuminate at later nodes; base retuse or emarginate or cordate at nodes 2–15, mostly cordate at later nodes; margins \pm irregularly serrate at nodes 1–3, becoming \pm doubly serrate at later nodes. Teeth irregularly spaced and variably sized at nodes 1–10, becoming \pm regularly spaced at later nodes; mostly 4–15 per side at first node, to ≈ 50 per side at nodes 1–10, and to > 100 per side at later nodes; margins mostly curved, proximal side longer than distal side; apex acute to short-acuminate; sinus angular. Blades green above, lighter below; flat between the veins when fresh; membranous; with pearl bodies common above and below on primary veins at nodes 1–10, especially basally above, and infrequent to common on primary and secondary veins at later nodes, but sometimes infrequent below; glabrous on blade above and below, glabrous to sparsely short-pubescent along margin; glabrous to sparsely short-pubescent on primary veins below at nodes 1–10, but only at base of primary veins above; glabrous to moderately short-pubescent on primary and secondary veins below at later nodes, but

glabrous or sparsely short-pubescent above along primary vein and densely pubescent at base; with short pellucid canals along margin drying harder than blade, canals absent or light yellow-orange at early nodes to mostly red-orange at later nodes; similar red-orange canals often conspicuous throughout blade of young leaves at later nodes. Hairs simple, erect to ascending, straight to curved, clear to cream-coloured. Pearl bodies minute, 0.05–0.075 mm in diameter, globular, short-stalked to sessile, erect, clear to white on immature leaves, becoming red-orange to brown with age. *Young leaves* plicate (lobes conduplicate-induplicate), densely pubescent, light green, with red-brown petioles, rigid, erect then \pm horizontal, produced continuously before or after previous leaf full-size. *Venation* palmate, 3- to 5-veined; actinodromous, basal, perfect and marginal. Primary veins 3 at nodes 1–3, 3 to 5 at later nodes; moderate-sized; impressed above, prominently raised below; central primary vein straight to slightly curved; lateral primary veins basal, diverging at moderately acute angles, straight to slightly curved, terminating at apex of lobes, sometimes only slightly thicker than secondary veins at first node. Secondary veins moderate-sized; 4–8 on central lobe and 1–3 on lateral lobes on leaves at first node, 6–15 on central lobe and 2–8 on lateral lobes at nodes 2–10, to 28 per lobe at later nodes; mostly alternate; mostly $\frac{1}{6}$ – $\frac{1}{3}$ length of blade, rarely to $\frac{2}{3}$ at first node, longest centrally on centre lobe; slightly curved; diverging at moderately acute angles; open, terminating at margin in tooth or sinus; impressed above, slightly raised below. Inter-secondary veins occasional. Tertiary veins reticulate. *Petioles* 10–200 mm long, \leq 42 mm long at nodes 1–10; straight, circular in t.s.; shallowly channelled; glabrous below, densely minute- to short-pubescent above at early nodes becoming \pm glabrous except densely pubescent apically at later nodes; with abundant pearl bodies above and below. *Stipules* paired; 0.3–1.8 mm long at nodes 1–10, to 5 mm long at later nodes; simple; triangular, keeled; apex acute to acuminate; deciduous to \pm persistent, papery; short-pubescent along margin and at apex, with pearl bodies along margin; green becoming brown, with red-orange canals along margin.

SAP. Resinous, drying orange-brown in stems and roots.

ODOUR. Unpleasant in hypocotyl and roots.

ARCHITECTURE. Koriba's model (Hallé et al., 1978). Trunk axis initially monopodial and orthotropic to at least 81 cm tall; eventually sympodial, one of the 2–6 branches at each tier becoming erect (Hallé et al., 1978). Branches orthotropic, \pm verticillate (Hallé et al., 1978). No major branches were produced on our seedlings, all \leq 81 cm tall. Proleptic branches, produced after apical meristem damaged, have 3–4 stipule-like scales toward base, produce several smaller leaves with fewer lobes than those formed before damage. Leaves held horizontal to descending.

Ecology

PHENOLOGY. Fruits mature during the late dry season, mostly after March in Panama (Croat, 1978), about 1–2(–4) months after peak flowering, while the tree is leafless (Poppendieck, 1981; Janzen, 1983; Bullock & Solis-Magallanes, 1990). Most seeds are shed before the rainy season begins (Poppendieck, 1980).

DISPERSAL. When ripe, capsules are dry, with outer valves dark brown, spreading and alternating with yellow-brown

membranous inner valves. Seeds are wind-dispersed floaters (Augsburger, 1988), being gradually liberated from the partially opened fruit (Poppendieck, 1981). In Costa Rica, seeds are eaten by spiny pocket mice (Janzen et al., 1990).

GERMINATION. Seeds have hard, impermeable seed coats. The chalazal plug must become loosened before imbibition and germination can occur, which may occur rapidly by fires frequent in their secondary habitats or more slowly by other factors. Germination of freshly collected, untreated seeds was low in sun and shade (\leq 17%), asynchronous over a 35 week period, and bimodal: a few seeds (4–9%) germinated in the first 3 weeks in sun (9 weeks in shade), the rest (8–12%) after a gap of 10–12 weeks. In a later seed collection, a hot water pretreatment increased germination over controls in both sun and shade (50% vs 4%): germination was still asynchronous (but not bimodal) over the 23 week period and was slightly faster in sun (7 weeks) than shade (9 weeks). Ricardi et al. (1987) also report low germination (7%) in the first three weeks. Seeds stored at room temperature were $>$ 95% viable after nearly 10 years (Garwood & Lighton, 1990), germinating in 7–10 days without treatments (Garwood, unpublished data).

ESTABLISHMENT. Seedlings are extremely shade intolerant and probably require large gaps to survive (Augsburger, 1984).

DISCUSSION

The gross morphology of seeds of *Bixa urucurana* Willd. is very similar to that of *B. orellana* L. (Dathan & Singh, 1972; Corner, 1976), including a complex chalazal plug, an embryo with cotyledons asymmetrically bent under the chalazal plug, and a sarcotesta formed by large pigment-containing cells. Seeds of the five species in the genus differ slightly externally in size and colouring of the testal pigments (Baer, 1976). The dry seeds of *B. urucurana* are red-brown to orange-brown (Macbride, 1941; Molau, 1983; this study); when rehydrated, seeds from my collections became bright yellow. Dry seeds of *B. orellana* are usually orange-red or red (Macbride, 1941; Corner, 1976; Molau, 1983); when rehydrated, seeds from a commercial source (purchased at a Mexican-American grocery) turned bright red (Garwood, personal observation). These colour differences may reflect differences in the relative amounts of bixin, a reddish oil-soluble pigment, and orellin, a yellowish water-soluble pigment, in the testa. As there were few seeds on other BM collections of *B. urucurana*, I have not yet determined whether this trait is characteristic of the species.

Seeds of *Cochlospermum vitifolium* (Willd.) Spreng. are similar in gross morphology to those described for *C. religiosum* (L.) Alston (= *C. gossypium* DC., Poppendieck, 1980), including a complex chalazal plug, curved form with curved embryo, long testal hairs, and a thick tegmen (Dathan & Singh, 1972; Corner, 1976). Seeds of the other ten species in the genus are similar (Poppendieck, 1980). The unique and complex chalazal foramen and plug of the exotegmic seeds most strongly link the Cochlospermaceae and Bixaceae (Corner, 1976); other shared characters and differences between the two families are reviewed by Poppendieck (1980) and Cronquist (1981).

Seedlings of *Bixa urucurana* Willd. and *Cochlospermum vitifolium* (Willd.) Spreng. share the following characters: cotyledons are phanero-epigeal, foliaceous, persistent, petiolate, estipulate and glabrous; and leaves are simple, alternate and spiral, long-petiolate, stipulate, palmately veined, mostly ovate to widely ovate, and basally cordate at least at early nodes. Leaves of both species and cotyledons of *B. urucurana* contain idioblasts: these are discussed in more detail below. The two species differ in the following traits. The cotyledons of *B. urucurana* are ovate, palmately veined and conspicuously thick-lined (faintly pellucid) on the lower surface (see below), while those of *C. vitifolium* are narrowly ovate, pinnate-veined and lack lines or punctations, pellucid or not. All seedling and juvenile leaves of *B. urucurana* are entire and not lobed or parted, whereas the first leaves (eophylls) of *C. vitifolium* are irregularly serrate, usually 3-lobed or 3-cleft, and later juvenile leaves are 3- to 5-parted.

Previously published short descriptions of seedlings of *Cochlospermum vitifolium* agree with our description, except that Duke (1969) reported the cotyledon venation as uninnervated and Ricardi et al. (1987) did not detect stipules on the eophylls. These differences might be attributed to the fact that the primary and secondary veins are weak, but clearly visible under a strong light source, and the stipules fall off as the leaf expands, although a stipule scar is evident at the first node on my collections. A short description of the seedling of *Bixa orellana* L. (Duke, 1969) agrees with that given for *B. urucurana*, except that cotyledons are described as punctate-lineate and the illustrated cotyledons are widely ovate rather than ovate.

Leaves of *Bixa* and *Cochlospermum* have branched unicellular secretory idioblasts and canals in the spongy mesophyll (Keating, 1970). In leaves of *B. urucurana* seedlings, I found irregular, circular or elliptic pellucid punctations, < 0.1 mm long, which were sometimes associated with pellucid branched or unbranched canals. Punctations and canals were scarcely visible on the blade above (except when back-lit), but were conspicuous on the blade below, light orange-brown or green-brown. When back-lit, punctations were usually translucent yellow-green at early nodes to light orange-brown at later nodes, but sometimes opaque and dark brown-orange at later nodes. On the cotyledons, the idioblasts are much larger, to 0.5 × 0.1 mm long, thick and elongate, more or less parallel to the midvein; they were scarcely visible on the upper surface (even when back-lit), but conspicuously light yellow-brown below, and translucent brown-orange when back-lit. In leaves of *C. vitifolium* seedlings, I found faintly pellucid canals along the margins, which were absent or light yellow at early nodes to red-orange at later nodes. Similar canals were sometimes conspicuous throughout the blade of young expanding leaves at later nodes. No canals were found in the cotyledons.

Leaf pubescence differs greatly between the two genera (Keating, 1970; Poppendieck, 1980), with *Bixa* having multicellular peltate scales on the blade and veins of the leaf undersurface and *Cochlospermum* having unicellular simple hairs as well as multicellular globular hairs. On seedlings of *B. urucurana*, Dempsey & Garwood (1994) found that the peltate scales are much smaller and sparser than those on adults: they discuss the systematic significance of these ontogenetic changes.

The presence of multicellular globular hairs in *Cochlospermum vitifolium* has not been noted in standard floras (Robyns, 1967b; Croat, 1978; Poppendieck, 1981), although

they have been briefly discussed in anatomical studies and monographs of the family (Keating, 1970; Poppendieck, 1980). On seedlings of *C. vitifolium*, I found that the multicellular globular hairs were 0.050–0.075 mm in diameter and most abundant on the youngest stem internode, and on stipule margins, petioles and primary and secondary veins of expanding leaves, but often persisted on mature leaves and nodes. Globular hairs on young leaves of adult specimens examined at the BM were in the same size range (Garwood, personal observation; see also Keating, 1970: fig. 4), although Poppendieck (1980: fig. 46) illustrates hairs up to 0.5 mm in diameter; these were initially abundant, especially at the base of the primary vein, but fewer were found on mature leaves. Poppendieck (1980) and Keating (1970) called these hairs vestigial, but they might be fully functional 'pearl bodies' as described by O'Dowd (1982). Pearl bodies are typically 0.5–3.0 mm long, uni- or multi-cellular, spherical or club-shaped with short stems, easily detached from the leaf, lipid-rich, colourless to opaque, lustrous and 'pearl'-like, and often produced on the youngest leaves or near extrafloral nectaries or domatia; they occur primarily in tropical taxa, particularly those from second-growth habitats (O'Dowd, 1982). Because they are rapidly removed by ants in the field as a source of food, pearl bodies are often absent or scarce on plants in their natural habitats and on herbarium specimens. Except for their small size, the globular hairs on *C. vitifolium* fit the morphological description of pearl bodies. Documentation of removal by ants or mites (given their small size) and characterization of the cell contents will be necessary to confirm their biological function. Poppendieck (1980) assumed that they contained the same clear gum or resin as the fluid-containing idioblast canals of the leaf: this has not been reported for pearl bodies (O'Dowd, 1982).

Saplings of *Bixa urucurana* have large extra-floral nectaries below the stipule scar (Fig. 1R). I found glands were absent on the first ten leaf nodes above the cotyledons, but were well-developed and secretory above node 20. They actively secreted nectar when less than 3–4 nodes below the youngest leaf, then became inactive. Similar glands occur on adult specimens of *B. urucurana* and *B. orellana* examined at BM (Garwood, personal observation) and have been reported for all species of *Bixa* except *B. excelsa* Gleason & Krukoff (Baer, 1976). Ant attendance at similar glands on the fruit pedicel of *B. orellana* sensu lato increases the proportion of flowers maturing fruits (Bentley, 1977), because the species of ants present remove or deter flowering-eating insects. Ants attending the glands on the stems of saplings probably reduce leaf herbivory in a similar way. This is another vegetative trait of ecological importance not described in the standard floras (Macbride, 1941; Standley & Williams, 1961; Robyns, 1967a; Croat, 1978; Molau, 1983) or a recent field guide emphasizing vegetative characters (Gentry, 1993).

The seedling characters discussed above do not provide additional evidence for a closer link between the Bixaceae and Cochlospermaceae. Shared seedling-specific traits are usually those common throughout the angiosperms, such as petiolate, estipulate, foliaceous cotyledons. The taxa often differ in less wide-spread seedling-specific traits, such as the presence of pinnate venation or linear punctations in the cotyledons. Many of the vegetative differences and similarities noted by Keating (1970) and Poppendieck (1980) for adult stages, such as idioblasts, secretory canals, pubescence and leaf lobing, are already manifest at the early seedling stage.

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A study of *Bixa* (Bixaceae), with particular reference to the leaf undersurface indumentum as a diagnostic character

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CONTENTS

Introduction	173
Materials and methods	174
Results	175
Discussion	176
Appendix	178
References	179

SYNOPSIS. In the course of preparation of an account of Panamanian *Bixa urucurana* Willd. for the *Seedling Flora Project*, differences in leaf undersurface indumentum were found between adults and juveniles. We describe the pattern of variation of indumentum between species within the genus and between developmental stages within *B. urucurana*. We conclude that leaf undersurface indumentum is a useful diagnostic character for the adult stages of the genus but not the juvenile stages.

INTRODUCTION

Bixa is the only genus of the small woody family, Bixaceae which is widespread in tropical America and frequently cultivated throughout the tropics. The genus has often been treated as one highly variable species, *Bixa orellana* L. sensu lato (Eichler, 1871; Kuntze, 1891; Warburg, 1895; Standley & Williams, 1961; Robyns, 1967; Croat, 1978) or as five separate species (Macbride, 1941; Baer, 1976; Molau, 1983). Primarily fruit and indumentum characters have been used to distinguish different species. Linnaeus' (1753) protologue of *B. orellana* simply described the capsules as 'chestnut-like'. Willdenow (1809) described a second species, *B. urucurana* from Brazil, defining it by the 'white' scales densely covering the leaf underside. This species has frequently been reduced in rank to a variety of *B. orellana*, especially in Central America (Kuntze, 1891; Standley & Williams, 1961; Robyns, 1967). In 1831, Don published a description of *B. platycarpa* Ruiz & Pav. from Peru, which had flat, kidney-shaped fruits with very few bristles. Triana (1858) described *B. sphaerocarpa* from Nouvelle-Grenade (now Colombia), having scaly leaf undersides and spherical capsules, but this was later reduced to a synonym of *B. urucurana* (Pilger, 1925; Baer, 1976). Huber (1910) described *B. arborea*, having a kidney-shaped, dorsally compressed capsule with a wrinkled surface. Finally, *B. excelsa* Gleason & Krukoff was described in Gleason (1934), and is characterized by reniform capsules densely covered by glandular trichomes. Although the original descriptions of the three species restricted to the Amazon basin (*B. arborea*, *B. excelsa*, *B. platycarpa*) all refer to a

more or less kidney-shaped fruit, there are other defining features which separate them as species. Baer (1976) contends that they are diagnosable on fruit shape when this is more accurately defined. Other diagnostic characters include fruit ornamentation, dehiscence, life-form, and the size and density of trichomes on the undersurface of the leaf (see Table 1 for a summary of these).

The primary taxonomic difficulty in the genus is separating *Bixa orellana* and *B. urucurana*. There is a high degree of variation between cultivars of *B. orellana*, especially in capsule shape since this has been the subject of artificial selection. Baer (1976) discusses possible intermediates or hybrids between *B. orellana* and *B. urucurana*, known predominantly from Panama and Costa Rica. These apparently have trichomes of intermediate size and density, relatively short, subspherical fruits with slender spines and intermediate numbers of seeds.

The variation in leaf indumentum is our principal concern. The undersurfaces of leaves of all five species of *Bixa* have peltate scales, which are circular discs supported on short obconical stalks about 20 µm long. They are red-brown in colour and formed of an outer ring of cells with a central circular area which is more densely pigmented. In *B. urucurana*, the scales are large, with several concentric rings of cells around the central core, irregular in outline and funneliform. Its scales are also very densely packed, giving a tawny-brown appearance to the undersurface of the leaf. (Willdenow's (1809) original description of white scales probably referred to a shiny appearance, observed due to reflection of incident light at certain angles).

Our study is based on herbarium material collected and

Table 1 Summary of life form, fruit and scale characters of the five *Bixa* species. (Baer, 1976; Molau, 1983; Macbride, 1941)

Species	Fruit shape		Spines	Dehiscence	Habit	Trichome	
	l.s.	t.s.				diameter (μm)	density (per mm^2)
<i>B. arborea</i>	subreniform	circular	absent	D	tree	69	12
<i>B. excelsa</i>	oblate	circular	stout, with glandular pubescence	D	tree	54	6
<i>B. orellana</i>	oblate/cordate	circular	absent or slender	D	shrub	64	19
<i>B. platycarpa</i>	circular	flat	absent	D	tree	63	50
<i>B. urucurana</i>	circular/depressed oblate	circular	tapered	I	shrub	94	156
<i>B. 'intermediates'</i>	oblate	circular	slender	D	shrub	80	59

Dehiscence: D= dehiscent, I= indehiscent. Trees are above 30 m at maturity, shrubby species grow to about 10 m. Trichome diameter is a mean (n unknown) and density 'representative' (taken from Baer, 1976).

grown in Panama for the *Seedling Flora Project* (see Garwood & Humphries, 1993). Accessions from this area have often been attributed to *Bixa orellana* L. sensu lato (Robyns, 1967; Croat, 1978). Our adult collections seem to refer to *B. urucurana* on the basis of both fruit and indumentum characters. However, we observed fewer and smaller scales on juvenile stages of the progeny of this adult (see description in Garwood, 1994) and felt that these observations merited further investigation. We pursued three main lines of enquiry: A) Within *B. urucurana*, are there significant differences in scale diameter and density at different positions across the lamina of the leaf or between different stages of development? How is variation in scale diameter apportioned between the central core and outer annulus of the scale? B) Do differences in scale density and diameter within juvenile individuals follow any trends associated with either leaf node or size? and C) How much variation in scale density and diameter is there between adults of the five different species of *Bixa* across their geographical range and is there any evidence for the existence of intermediates between *B. orellana* and *B. urucurana*?

MATERIALS AND METHODS

Seeds were collected from one individual of *Bixa urucurana* along the Chagres River, Gamboa, Panama in May 1986 and April 1987. These seeds were germinated in a screened growing house on Barro Colorado Island (BCI), Panama. The resulting juveniles were harvested at intervals and pressed to provide herbarium specimens of various stages of development. A voucher specimen was also collected of the adult in May 1986. Two *Bixa* seedlings were collected from a beach on BCI, but the parental seed source was unknown.

A) To determine whether significant variation occurred in *Bixa urucurana* in scale size and density between different positions on the lamina, and between stages of development, and to ascertain where scale diameter variation arises (whether central core or outer annulus), we took an initial sample of two leaves from each of five juveniles and one of the beach seedlings. This was also undertaken for two leaves of the adult voucher specimen. Scale density was measured as the number of scales per mm^2 with a photogratule on a Leica dissecting microscope. Ten measurements were made at each of three positions across the lamina; at the edge, in the middle and adjacent to the primary vein. Scale diameter was measured using an eyepiece graticule in a compound

microscope at $\times 125$ magnification. Small squares (about 1 mm^2) of leaf tissue cut from the three positions described above were placed on a glass slide and the diameter of both the dark, central portion and the entire scale were measured for ten scales at each position. The results were analyzed as follows: i) two-way (Model II) analysis of variance (ANOVA) was used to partition the variance in scale density, scale core diameter and total scale diameter into components attributable to lamina position, leaf and position \times leaf interaction effects. ii) three-level nested ANOVA (Model II) was employed to partition the three scale variables into the effects of stage, individual and leaf. Variance components were calculated by the methods of Sokal & Rohlf (1981). These results and those of the following investigations were all analyzed using SYSTAT (Wilkinson, 1990).

B) To determine whether variation in scale density and diameter varied with leaf node and size within an individual, two of the largest juveniles were further studied, repeating the above measurement procedures, for edges of leaves only, for all leaves available on the specimens. The leaf length and width and the node from which the leaf originated were recorded. From this data, means and standard errors were calculated for each variable at each node and the results plotted. Relationships between scale diameter, scale density, leaf node and width, were tested by a linear regression for multiple values of y per x: resulting regression mean squares were tested over the deviation mean square and the proportion of variance attributable to the linear regression was evaluated by the coefficient of determination (r^2) (Sokal & Rohlf, 1981). The relationship between leaf-length and width was quantified using the Pearson product-moment correlation coefficient (r).

C) To estimate the variation in scale size and density in the genus *Bixa* as a whole, a selection of specimens in the BM herbarium was chosen (see Appendix). Five edges of leaves were measured for scale density and diameter in the same manner as described above, for one leaf of each of the chosen specimens. Specimens of *B. orellana* from Central America, South America and the West Indies and *B. urucurana* from Central and South America, were chosen from those with reliable recent determinations or mature fruits. For the other three Amazonian species, all specimens with leaf undersurfaces uppermost were studied, including several type specimens, since little material was available. Mean scale density and mean total scale diameter were calculated for each of these specimens.

Table 2 Results of two-way ANOVA (Model II) of effects of position (edge, middle or vein) and leaf on scale density and diameter. Two leaves on each of five juveniles and one adult were included.

Source	DF	Scale diameter								Scale density			
		Total scale				Central core				MS	F	P	%
		MS	F	P	%	MS	F	P	%				
Leaf	11	254.23	221.07	***	91.00	3.05	3.70	**	12.76	6165.03	311.66	***	94.39
Position	2	2.94	2.55	ns	.16	.61	.74	ns	0.00	74.59	3.77	*	.21
Leaf * position	22	1.15	1.50	ns	.41	.82	1.75	*	6.08	19.78	1.83	**	.41
Error	324	.77			8.31	.47			81.16	10.82			4.98

DF, degrees of freedom; MS, mean squares; F, F-statistic; P, probability: *, $0.01 < p \leq 0.05$; **, $0.001 < p \leq 0.01$; ***, $p \leq 0.001$; ns, not significant; %, percent of total variance contributed by variance component of each source.

Table 3 Results of three-level nested ANOVA (Model II) for stage (adult vs juvenile), individuals within each stage, and leaves within individuals, of scale diameter and density.

Source	DF	Scale diameter								Scale density			
		Total scale				Central core				MS	F	P	%
		MS	F	P	%	MS	F	P	%				
Stage	1	913.90	253.65	***	96.11	3.01	1.41	ns	3.97	17184.20	48.45	**	88.55
Individual	4	3.60	1.16	ns	.08	2.13	3.92	**	13.03	367.66	.68	ns	0.00
Leaf	6	3.14	3.69	**	.81	.40	.72	ns	0.00	542.11	44.34	***	9.30
Error	108	.85			3.00	.55			83.01	12.23			2.15

DF, degrees of freedom; MS, mean squares; F, F-statistic; P, probability: *, $0.01 < p \leq 0.05$; **, $0.001 < p \leq 0.01$; ***, $p \leq 0.001$; ns, not significant; %, percent of total variance contributed by variance component of each source.

RESULTS

A) For scale density in *Bixa urucurana*, a two-way ANOVA (Table 2) indicated a significant effect of position, leaf and position \times leaf interaction. However, the greatest part of the variance is accounted for by differences between leaves (94%), and a very small portion is attributable to position on the lamina or the leaf \times position interaction. For total scale diameter, position and the interaction term are not significant, whilst most of the variation (91%) is again accounted for by differences between leaves. While leaf and leaf \times position interaction effects were significant, most of the variation (81%) in core diameter was among replicate scales on leaves. Since position did not appear to be an important effect, further sampling and analysis was carried out on the edge of the leaves only, as this was easier and caused less damage to the specimens.

The results of the three-level nested ANOVA are summarized in Table 3. There is significant variance in scale density and total scale diameter between adult and juvenile specimens of *Bixa urucurana*, and between leaves, but not between individuals. Most of the variation of total scale diameter (96%) and density (89%) is attributable to differences between adults and juveniles. The results for central core diameter are quite different. Only the difference between individuals is significant and most of the variation (83%) occurs within replicates on leaves. Since there was so

little variation in central core diameter, total scale diameter alone was used in further analyses.

B) The variation of scale density, scale diameter and leaf width with node for the two largest juveniles is shown in Fig. 1. Leaf age decreases with node number: because the youngest leaves at the highest nodes are still expanding they have a small width and a very high scale density and were excluded from the analysis. For fully expanded leaves, of both individuals, *Garwood* 1830D and *Garwood* 2085D, mean scale density increases with leaf node ($F_{(1,12)} = 6.601$, $p = 0.025$; $F_{(1,7)} = 41.730$, $p = 0.001$, respectively), although the linear regression accounts for only a proportion of the total variation ($r^2 = 0.244$ and 0.588 respectively). The increase in scale density is independent of leaf width: a linear regression of scale density on leaf width was not significant in either individual ($F_{(1,12)} = 0.794$, $p = 0.500$; and $F_{(1,7)} = 1.391$, $p = 0.500$). We tested only leaf width, because leaf length was highly correlated with width in both individuals ($r_{(12)} = 0.892$, $p = 0.001$; and $r_{(7)} = 0.916$, $p = 0.001$). Scale diameter does not appear to have any significant trend associated with leaf node or size in either individual ($F_{(1,12)} = 3.966$, $p = 0.100$ and $F_{(1,7)} = 0.633$, $p = 0.500$ for node; $F_{(1,12)} = 0.148$, $p = 0.250$ and $F_{(1,7)} = 0.005$, $p = 0.75$ for width) and the proportion of variation accounted for by the linear regression was very low ($r^2 \leq 0.039$ for node; $r^2 \leq 0.002$ for width). The leaf dimensions of our juvenile specimens (11.5–22.6 cm long \times 8.7–16.7 cm wide) exceeded the range of our adult speci-

mens (9.4–13.6 cm long \times 5.0–9.7 cm wide) and are well within the published ranges for adults of the species (5.5–27 cm long \times 3–18 cm wide), (Standley & Williams, 1961; Robyns, 1967; Molau, 1983).

C) *Bixa orellana* and *B. urucurana* have the least certain specific status in the genus. On a plot of mean scale diameter versus mean scale density (Fig. 2a) specimens attributable to these taxa cluster into two groups (see Appendix for list of specimens), the lower being *B. orellana* and the upper *B. urucurana*, with two exceptions. Firstly, the Panamanian Fendler 328 specimen ('F' in Fig. 2a), the BM specimen of which consists of a mature *B. urucurana* fruit and a separate small non-fruiting branch, clearly groups with *B. orellana*. Baer (1976) placed a specimen from the same collection in *B. urucurana*. Secondly, our juvenile specimens of *B. urucurana* from Panama and the unidentified *Bixa* sp. seedlings from BCI clearly group at the lower end of the *B. orellana* range. In contrast, the (adult) parent is clearly in the *B. urucurana* group.

South American specimens of both *Bixa orellana* and *B. urucurana* group at the extremes of the ranges of both mean scale diameter and density. The Central American specimens of both taxa group towards the centre of the overall range of indumentum characters. West Indian specimens of *B. orellana* group closely with South American representatives of the same taxon.

Although there are too few specimens to form a reliable cluster, the three Amazonian tree species (*B. arborea*, *B. excelsa* and *B. platycarpa*) also cluster with *Bixa orellana* (Fig. 2b).

DISCUSSION

There is considerable variation in the indumentum of leaf undersurfaces in the genus *Bixa*. There are also several different trends in this variation which need to be considered and explained before the utility of indumentum differences as a diagnostic character of species can be evaluated.

Differences between positions on the same leaf were found to be much less significant than other effects (e.g. leaf, individual or age) for scale density and not significant for scale diameter. Baer (1976) stated that scale density increased near veins or at the base of the leaf, but we found little evidence for this in either adults or juveniles.

Both scale density and scale diameter are radically different between adults and juvenile stages of *Bixa urucurana*. On average, adult scales are more than twice as large and about four times denser than those of the juveniles. There is a slight overlap, however, between the ranges of density in adults

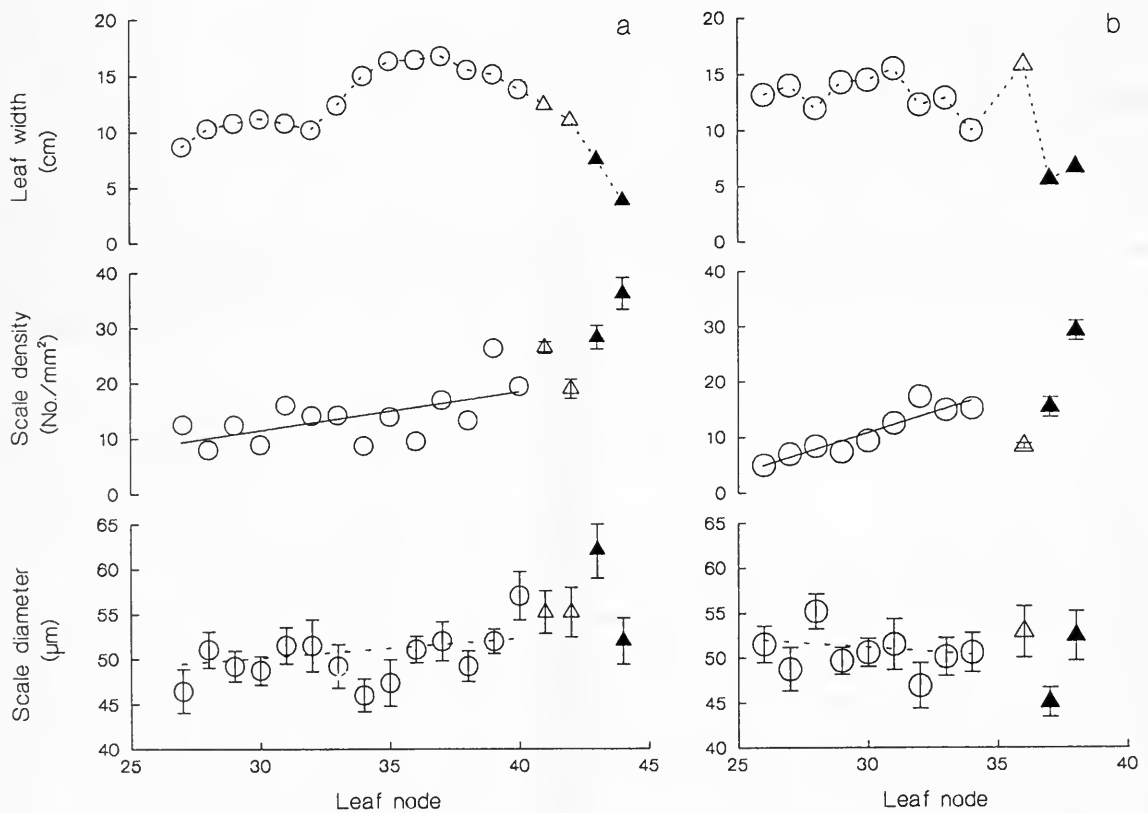


Fig. 1 Relationship of scale diameter, scale density and leaf width to leaf node in juvenile specimens.

(a) Juvenile *Garwood* 1830D.

(b) Juvenile *Garwood* 2085D.

(Open circles represent fully expanded leaves, filled triangles expanding leaves and open triangles 'borderline' leaves. Error bars for scale density and diameter represent the standard error of the mean and, where missing, the errors are smaller than the symbols. For scale diameter, the hatched line represents a non-significant linear regression. The linear regressions for scale density are significant ($p \leq 0.025$). Only fully-expanded leaves were included in the regression calculations.)

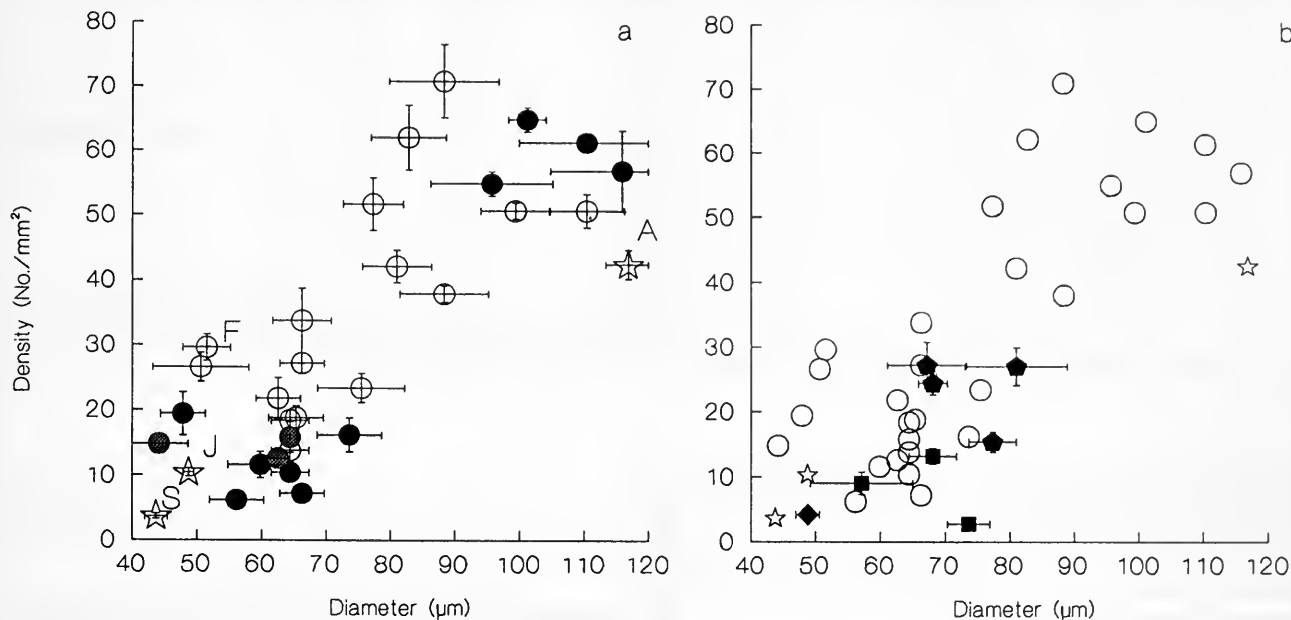


Fig. 2 Scale diameter versus scale density in *Bixa* spp. Mean \pm SE (N = 5 replicates on one leaf except for *Garwood* specimens marked by stars).

- (a) *B. orellana* and *B. urucurana*. (Filled circles represent South American collections, hatched circles West Indian collections and open circles Central American collections. Stars represent our Panamanian collections: A = Adult (N = 10 replicates from two leaves on one individual), J = Juvenile (N = 10 replicates from two leaves on each of five individuals) and S = *Bixa* sp. seedling (N = 10 replicates from two leaves on one individual). F = Panamanian specimen *Fendler* 328.
- (b) Five *Bixa* species. (Open circles and stars represent *B. orellana* and *B. urucurana* specimens from Fig. 2a; squares, *B. arborea*; pentagons, *B. platycarpa*; diamond, *B. excelsa*).

(27–65 scales per mm²) and juveniles (2–35 scales per mm²). There is no overlap between scale diameter of the juveniles (27.6–73.6 μ m) and the adults (82.8–147.2 μ m).

The difference in total scale diameter between adults and juveniles is accounted for by the outer portion or annulus of the scale: there is no significant difference in central core diameter between stages. In *Bixa urucurana*, the scales on adult leaves have a number of concentric rings of colourless cells around the dark central core (Baer 1976). Evidently, it is an increase in the number of these rings which increases overall scale size in the adults of this species. Although we observed these annuli in juvenile specimens, they were generally very narrow, comprising perhaps only one or two rings of cells and were occasionally completely absent, especially in the very young beach-collected seedlings.

The second trend within *Bixa urucurana* is that scale density increases with node number in juvenile specimens, whilst there is no clear trend in scale diameter with node number. However, since we found a significant difference in scale diameter between adults and juveniles, it would appear that changes in this parameter (i.e. the increase in number of rings of cells around the centre of the scale) must occur at some point between the two stages of plant development we studied. Further study of a range of intermediate, sapling stages would be required to ascertain whether there is a gradual increase in scale size with node. Scale diameter is not low due to small leaf size, since our juvenile leaves are generally larger than the adult leaves examined.

Thirdly, the comparison between our specimens and those of a sample from the BM herbarium shows that two distinct clusters of taxa are formed when mean scale diameter is

plotted against mean scale density (Fig. 2). The lower group with small, sparse scales includes all the specimens of *Bixa orellana* sensu stricto. The upper cluster of individuals with large, relatively densely packed scales, contains specimens which were originally variously identified as *B. orellana* sensu lato, *B. urucurana*, *B. orellana* var. *urucurana* or *B. sphaerocarpa* (see Appendix). We interpret these as *B. urucurana* since they form a close-knit group on the basis of indumentum characters and their fruit characteristics correspond, being subspherical, spiny and indehiscent. The problematic specimen, *Fendler* 328 ('F' on Fig. 2a) which Baer identified as *B. urucurana*, clearly groups with *B. orellana* on the basis of indumentum characters. However, there is a mature, subspherical capsule on the herbarium sheet which looks like that typical of *B. urucurana*. On closer inspection, it was noticed that the vegetative shoot on the herbarium sheet was non-reproductive and had never borne flowers or fruit; therefore, it must have been collected either from a completely different part of the same plant or even perhaps from a different individual than the fruit.

The South American specimens of the two shrubby species, *Bixa orellana* and *B. urucurana*, group at the extremes of the range of indumentum characters (Fig. 2a). Although the Central American specimens still form recognizable clusters with the conspecific specimens from South America, their indumentum characters tend to fall into the middle of the overall range for the two species. It would appear from Baer's (1976) estimates of scale density and diameter (Table 1) that some of the Central American specimens fall into his 'intermediate' category. However, his scale density estimate for *B. urucurana*, 156/mm², is inordinately high when compared to

our measurements: our highest mean value was 70 scales/mm² and our highest single value was 85 scales/mm². Unfortunately, because Baer does not give his sample sizes, it is difficult to compare the measurements. The fact that specimens of the two Central American species are much closer to each other than are those from South America, may suggest that there is some degree of intermediacy. Perhaps if we had sampled more specimens, we would have observed more of a continuum rather than two separate clusters. Since West Indian specimens of *B. orellana* group with South American specimens of the same taxon, it appears that dispersal (either naturally or through cultivation) has taken place directly from South America to the West Indies, bypassing Central America.

We conclude that the differences between indumentum characters in *B. orellana* and *B. urucurana* adults distinguish them as two separate species. This is reinforced by differences in fruit characters (see Table 1).

The three Amazonian tree species cluster with *Bixa orellana* and do not appear to be separable from it on the basis of indumentum characters alone, although it is recognized that the sample studied here is small.

It is apparent that *Bixa urucurana* manifests a broad range of scale diameter and density as it proceeds through its

development. The stages in this process apparently encompass all the variation observed in *B. orellana* and the Amazonian species. That four of the five *Bixa* species and the juveniles of *B. urucurana* have small sparse scales suggests that perhaps the large, densely packed scales of adult *B. urucurana* represent a more derived state.

The demonstration of the range of variation in indumentum characters through development within *Bixa urucurana* clearly shows that the utmost caution must be exercised when using them as diagnostic characters within the genus. It is important primarily to ensure that the leaf material studied comes from a mature individual.

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APPENDIX

Table of specimens examined.

Species	Collector(s)	No.	Country	Original ID	Later ID	Mean (SEM)	
						Scale density (No./mm ²)	Scale diameter (µm)
<i>B. arborea</i>	Ducke	8311	Brazil	A		13 (1.2)	68 (3.7)
	Huber	7827	Brazil	A		3 (1.0)	74 (3.3)
	Krukoff	8551	Brazil	A	A (DB '76)	9 (1.7)	57 (7.9)
<i>B. excelsa</i>	Krukoff	6831	Brazil	E		4 (0.5)	49 (1.8)
<i>B. orellana</i>	Barclay	425	Ecuador	O	O (UM '82)	10 (1.2)	64 (2.9)
	Barclay	851	Colombia	O	O (UM '82)	6 (1.3)	56 (4.2)
	Bunting & Licht	1070	Nicaragua	O		26 (2.2)	51 (7.4)
	Hahn	104	Martinique	O		15 (0.5)	44 (4.5)
	Hall & Bockus	7849	Colombia	OO		27 (1.6)	66 (3.4)
	Hartman	12006	Panama	O	O (RL '84)	19 (1.8)	65 (4.2)
	Jenman	5268	British Guiana	O		7 (0.8)	66 (3.4)
	Mexia	6435	Peru	O	O (UM '82)	16 (2.6)	74 (5.0)
	Nelson & Vargas	5072	Honduras	O	O (RL '91)	33 (4.9)	6 (4.5)
	Saunders	694	Honduras	O		23 (2.2)	75 (6.8)
	Tenorio & Miller	3313	Mexico	O	O (FR '83)	21 (3.1)	63 (3.4)
	Wagner	519	Puerto Rico	O		12 (0.8)	63 (1.8)
	Whitefoord	3169	Belize	O		18 (1.6)	64 (2.9)
	Whitefoord	4592	Dominica	O		16 (2.3)	64 (0.0)
	Williams	579	Bolivia	O		11 (2.0)	60 (5.0)
Williams	649	Bolivia	O		19 (3.2)	48 (3.4)	
Yuncker et al.	8404	Honduras	O		14 (3.0)	64 (2.9)	
<i>B. platycarpa</i>	Klug	3040	Peru	O	P (UM '82)	24 (1.8)	68 (0.3)
	Klug	4116	Peru	O	P (UM '82)	27 (3.5)	67 (6.1)
	Pavon	s.n.	Peru	P	P (UM '82)	27 (2.8)	81 (7.9)
	Ruiz & Pavon	s.n.	Peru	P	P (UM '82)	15 (1.5)	77 (0.7)
<i>B. urucurana</i>	Fendler	328	Panama	-	U (DB '76)	29 (2.0)	52 (3.7)
	Garwood	1830a	Panama	O	U (NG '93)	42 (2.2)	117 (3.5)
	Garwood (J)	1830b	Panama	O	U (NG '93)	8 (0.8)	42 (1.9)
	Garwood (J)	1830c	Panama	O	U (NG '93)	10 (0.6)	48 (1.8)

	<i>Garwood</i> (J)	1830d	Panama	O	U (NG '93)	18 (2.1)	52 (1.0)
	<i>Garwood</i> (J)	2085c	Panama	O	U (NG '93)	7 (0.4)	51 (1.5)
	<i>Garwood</i> (J)	2085d	Panama	O	U (NG '93)	9 (1.1)	51 (1.6)
	<i>Garwood et al.</i>	613	Costa Rica	O	U (RD '94)	51 (4.0)	77 (4.7)
	<i>Khan et al.</i>	875	Costa Rica	O	U (RD '94)	42 (2.4)	81 (5.4)
	<i>Krukoff</i>	1069	Brazil	OU	U (RD '94)	64 (1.9)	101 (0.9)
	<i>Marshall & Neil</i>	6620	Nicaragua	OU	U (RD '94)	37 (1.3)	88 (6.9)
	<i>Philipson et al.</i>	1445	Colombia	O	U (UM '82)	61 (1.1)	110 (10.5)
	<i>Pittier</i>	4581	Panama	OP	U (RD '94)	50 (2.5)	110 (5.8)
	<i>Proctor</i>	32394	Honduras	OU	U (RD '94)	50 (1.3)	99 (5.4)
	<i>Rombouts</i>	177	Surinam	O	U (RD '94)	54 (1.9)	96 (9.5)
	<i>Schmalzel</i>	994	Panama	O	U (RL '88)	70 (5.6)	88 (8.5)
	<i>Seymour</i>	s.n.	Nicaragua	O	U (RD '94)	61 (5.0)	83 (5.8)
	<i>Triana</i>	s.n.	Colombia	S	U (DB '76)	56 (6.2)	116 (11.1)
<i>B. sp.</i>	<i>Garwood</i> (S)	2439a	Panama	?	U?(NG '93)	4 (0.4)	44 (1.7)

Original ID codes: A, *Bixa arborea*; E, *B. excelsa*; O, *B. orellana*; OO, *B. orellana* var. *orellana*; OU, *B. orellana* var. *urucurana*; P, *B. platycarpa*; S, *B. sphaeocarpa*; U, *B. urucurana*. Where original determinations have been confirmed or changed, this is noted in the 'Later ID' column, giving date and identifier: DB, D. Baer; UM, U. Molau; RL, R. Liesner; FR, F. Ramos; NG, N. Garwood; RD, R. Dempsey. Mean scale densities and diameters are calculated from 5 edge measurements on one leaf for all specimens except *Garwood* 1830a, b, c & d, 2089c & d, and 2439a, for which means include 10 edge measurements on each of two leaves. (J), juvenile specimen; (S), seedling; (SEM), standard error of the mean.

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CONTENTS

- 101 **Observations on the benthic marine algal flora of South Georgia: a floristic and ecological analysis**
D.M. John, P.J.A. Pugh and I. Tittley
- 115 **Studies in *Pseudocyphellaria* (Lichens) IV. Palaeotropical species (excluding Australia)**
D.J. Galloway
- 161 **Morphology and ecology of seedlings, fruits and seeds of Panama: Bixaceae and Cochlospermaceae**
N.C. Garwood
- 173 **A study of *Bixa* (Bixaceae), with particular reference to the leaf undersurface indumentum as a diagnostic character**
R.E. Dempsey and N.C. Garwood