

A Revision of *Amansia glomerata* C. Agardh, *Amansia rhodantha* (Harvey) J. Agardh and *Melanamansia glomerata* (C. Agardh) R. E. Norris (Rhodophyta: Rhodomelaceae)

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Species of *Amansia* and *Melanamansia* from the tropical Pacific region have been re-examined, and compared with material from the Indian Ocean, Japan, Taiwan and the Philippines. All specimens examined from the Pacific region (except Hawaii and some from New Caledonia and Fiji) lack pseudo-pericentral cells, thus placing them in *Amansia*. *Melanamansia glomerata* is only reported from Hawaii, New Caledonia, Fiji, the Philippines, Vietnam, Malaysia and for the first time in the Indian Ocean from Kenya. Type material of *Amansia rhodantha* (Harvey) J. Agardh from Mauritius was compared and found not significantly different from the Pacific *Amansia* material (including type and isotype material of *Amansia paloloensis* South et Skelton from Samoa, which is reduced to synonymy), thus extending the distribution range of *A. rhodantha* as a pan-tropical entity.

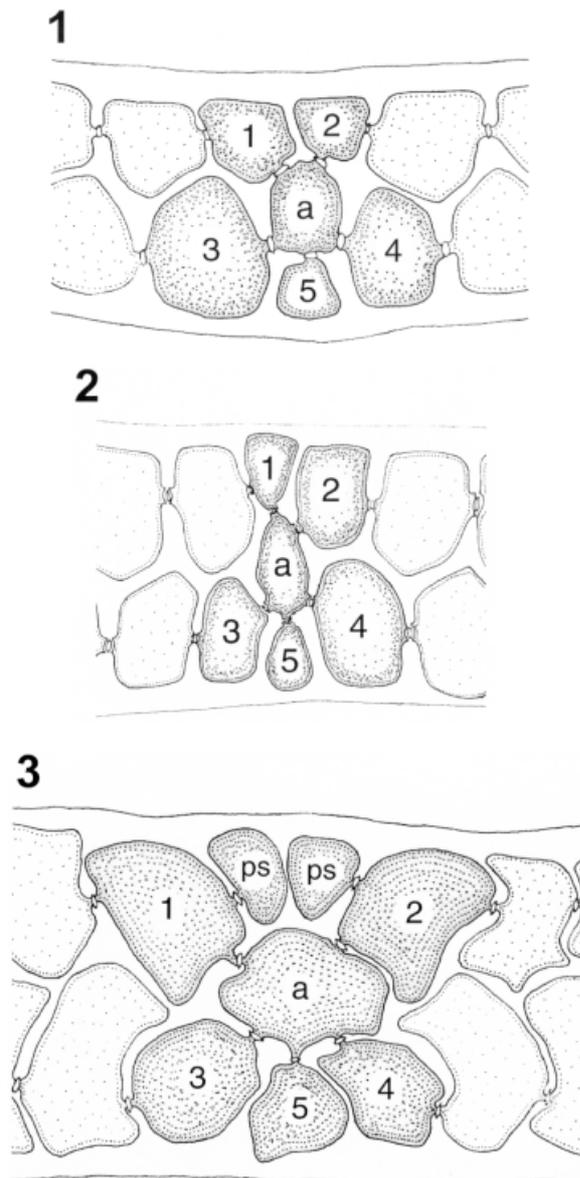
Introduction

The genus *Amansia* was erected by Lamouroux (1809: 322) and is placed in the tribe Amansieae of the family Rhodomelaceae (Hommersand 1963: 335). The tribe is characterised by dorsi-ventral, erect thalli arising in tufts from a common basal disc. Most genera have five pericentral cells around the axial cell (Figs 1, 2) except *Kuetzingia* Sonder and *Protokuetzingia* Falkenberg, which have six pericentral cells (Kylin 1956). The two first-formed pericentral cells lie on the dorsal side of the characteristically in-rolled apex of the mature lanceolate blades. In *Amansia* the dorsal and dorsi-lateral pericentral cells further divide to form immediately behind the apex a distromatic wing or ala, whose cells are arranged in alternate layers, with secondary lateral pit-connections (Fritsch 1945: 570).

Recently, Norris (1988b, 1995) re-examined species of *Amansia* in the Indian Ocean and Hawaii, and discovered that some members of this genus differed consistently by having the first and second pericentral cells each producing a lateral pseudo-pericentral cell lying adjacent, but not connected to, the axial cell (Norris 1988b: 214; Fig. 3). Species previously ascribed to *Amansia* that had these pseudo-pericentral cells were transferred to a new genus (*Melanamansia* R. E. Norris 1988b: 217). Notably, Hawaiian plants previously ascribed to the common tropical species *Amansia glomerata* C. Agardh (whose type locality is Hawaii) were transferred to *Melanamansia glomerata* (C. Agardh) R. E. Norris, while Indian Ocean '*Amansia glomerata*' were put under the earlier name *Amansia rhodantha* (Harvey) J. Agardh based

on their lack of pseudo-pericentral cells (Norris 1995). The genus *Amansia* currently consists of four species, the Caribbean *A. multifida* Lamouroux (the type of the generic name), *A. loriformis* R. E. Norris and *A. rhodantha* (Harvey) J. Agardh from the Indian Ocean and Malaysia, and *A. paloloensis* South et Skelton from Samoa. *Melanamansia* currently consists of twelve species, *M. daemellii* (Sonder) R. E. Norris, *M. glomerata* (C. Agardh) R. E. Norris, *M. japonica* (Holmes) R. E. Norris, *M. mamillaris* (Lamouroux ex C. Agardh) R. E. Norris, *M. pinnatifida* (Harvey) R. E. Norris, *M. pumila* (Sonder) R. E. Norris, *M. scalpellata* (Tanaka) R. E. Norris, *M. seagriefii* R. E. Norris, *M. serrata* (Harvey) R. E. Norris and *M. mitsuui* (Tanaka) Yoshida.

Following these revisions by R. E. Norris, several authors (Yoshida *et al.* 1995, N'Yeurt *et al.* 1996, Payri and N'Yeurt 1997, Millar 1999, Millar *et al.* 1999) made the nomenclatural change from *Amansia glomerata* to *Melanamansia glomerata* in their checklists and herbarium collections from the tropical Pacific, but until recently no detailed studies verifying these changes as correct have been done. In 1995, samples of '*Amansia glomerata*' from Rotuma Island (north of Fiji) were sent to Dr R. E. Norris, who confirmed (pers. com.) that pseudo-pericentral cells were present, and on the basis of this assumed finding the name *Melanamansia glomerata* was used in later publications (N'Yeurt 1996, N'Yeurt *et al.* 1996). Later, in the course of on-going investigations on the Samoan algal flora, South and Skelton (1999) found a species of *Amansia* lacking pseudo-pericentral cells, which they described as new (*A. paloloensis* South et Skelton), while in Malaysia and Vietnam (Masuda *et al.* 2000, Masuda



Figs 1–3. Arrangement of pericentral cells in species of *Amansia* and *Melanamansia* (modified from Norris 1988b; a = axial cell; 1–5 = order of formation of pericentral cells; ps = pseudo-pericentral cells).

Fig. 1. *Amansia rhodantha* (Beqa, Fiji, SUVA-A 5436L). Fig. 2. *Amansia rhodantha*, showing intrusion of the first derivative of the first-formed pericentral cell into the axial ring (Suva, Fiji, SUVA-A 5438L). Fig. 3. *Melanamansia glomerata*, cross section of the lectotype from the Hawaiian Islands (LD 42600) showing the first two dorsal pericentral cells each developing a pseudo-pericentral cell (ps) that lies adjacent to the axial cell.

pers. com.) recent studies found both *Melanamansia glomerata* and *Amansia rhodantha* (Harvey) J. Agardh to co-exist in the flora. Most recently, a detailed morphological and taxonomic study on some selected members of the Amansieae (Wilson and Kraft 2000) echoed the opinion that the genus *Amansia* in Australia was in need of critical revision.

In order to clarify the taxonomy of species hitherto ascribed to *Melanamansia glomerata*, *Amansia rhodantha* and *Amansia glomerata*, it was decided to revise records in the light of recent findings, in particular paying attention to important anatomical features such as the presence or absence of pseudo-pericentral cells and the number of segments between lateral veins of the blade (Norris 1995). The results of these investigations are described below.

Material and Methods

Specimens were collected by reef-walking, snorkelling or SCUBA diving, and stored in 5% buffered Formalin in seawater prior to shipment to the laboratory. Sections were made using a freezing microtome, and stained with cotton blue in lactophenol or 1% acidified aniline blue in 60% clear corn syrup. Prepared slides were examined using a Zeiss compound microscope, and a camera-lucida attachment was used to make anatomical drawings. Macrophotography was done with a Nikon F2A in conjunction with Kodak Plus-X pan 125 film, developed and printed in the laboratory. Photomicrographs were obtained using an Olympus BX-50 compound microscope. 'AI' and 'CG' refer to specimens housed at IRD, Nouméa, New Caledonia; otherwise as in Holmgren *et al.* (1981).

Results

Representative material examined

Amansia rhodantha

- Japan: Hanasado Beach, Tanegashima Island, Kagoshima: 9 August 1959, leg. Y. Sakai and S. Enomoto (SAP); Furusato, Okinoerabujima Island (60 km north of Okinawa), 13 May 1982, leg. M. Baba (SAP 056160); Okidomari, Okinoerabujima Island (60 km north of Okinawa) 27 Sept. 1989, leg. M. Baba (SAP 056163).
- Taiwan: Anon., 25 October 1984 (SAP 046978).
- French Polynesia: Moorea, 1984, leg. C. E. Payri (8/84, in EPHE); Taharaa, Tahiti, 6 Jun. 1997, leg. A. N'Yeurt (UPF 347); Punaauia, Tahiti, 19 Mar. 1998, leg. A. N'Yeurt (UPF 584).
- Cook Islands: Ngatangia, Rarotonga, 9 Feb. 1999, leg. A. N'Yeurt (SUVA-A 5128).
- Samoa: Palolo Deep Reserve, 2 Jul. 1998, leg. P. A. Skelton and Dave [SUVA-A 1565 (holotype), SUVA-A 1566 (isotype), SUVA-A 2402 (Lectotype) and liquid-preserved isotypes 5479L (tetrasporic), 5480L (cystocarpic), 5481L (spermatangial)]; Palolo Deep, deep algal rim, 2 Jul. 1998, leg. P. A. Skelton and Dave (SUVA-A 1567); 11 Jul. 1998, leg. P. A. Skelton, M. Tomblinson and T. Rintels (SUVA-A 3891, 3892, 3893, 3895, 3896, 3897); 18 Sep. 1998, leg. P. A. Skelton, U. Afiti and D. Faletose (SUVA-A 3894, 3898, 3899).

Table I. Average values of selected characters for *Amansia paloloensis*, *Amansia rhodantha* and *Melanamansia glomerata* surveyed in this study.

Species	Thallus height (cm)	Blade width (mm)	Blade length (mm)	Serrations (1–3)*	Cortication (1–3)*	Rosettes (1–3)*
<i>Amansia rhodantha</i>	39.7	3.5	18.1	2	2	2
<i>Amansia paloloensis</i>	54.2	3.3	22.9	2	2	2
<i>Melanamansia glomerata</i>	53.6	2.9	11.7	1	2	2

* As measured on an index of (1 = little) to (3 = pronounced)

- Rotuma: Hoféa, Hapmak, 3 and 5 March 1992, leg. A. N'Yeurt (SUVA-A 346, 347); Lopta, 18 March 1992, leg. A. N'Yeurt (SUVA-A 5437L).
- Fiji: 'Feejee', 1838–42, leg. Wilkes Exploring Expedition (US 04057a); Nanuyalevu, Yasawa Islands, 13 July 1972, leg. B. Carlson (SUVA-A 281); Rukuruku Village, Ovalau, 14 Feb. 1982, leg. S. Villeneuve (SUVA-A 1737); Naukathura Island, Yasawa Group, 25 Feb. 1982, leg. S. Villeneuve (SUVA-A 1774); Tangangge, Viti Levu, 3 and 15 Oct. 1985, leg. H. Kasahara (SUVA-A 1012, 1069); Vatualailai, Viti Levu, 16 Oct. 1985, leg. H. Kasahara (SUVA-A 1013, 1067); Suva Barrier Reef, leg. D. W. Keats, 21 Sep. 1994 (SUVA-A 797); Suva Reef, 3 Feb. 1995, leg. A. Ballou (SUVA-A 5438L); Namada, Viti Levu, 14 March 1998, leg. P. A. Skelton and G. R. South (SUVA-A 2460); Beqa Lagoon, 25 September 1999, leg. C. Garrigue (SUVA-A 5436L).
- New Caledonia: Lajeu Sudouest, n.d., leg. C. Garrigue (CG 77c, CG 77b); Chesterfield, 17 Jul. 1984, leg. C. Garrigue (CH1).
- Philippines: Gao-oa, Pagodpud, Ilocos Norte, 11 Feb. 1973, leg. P. Moreland (US 50851); Solong-On, Siquijor Is., 10 May 1978, leg. SIPHILEXP-78 (US 088534); Canipo Is., Cuyo, Palawan, 23 May 1978, leg. SIPHILEXP-78 (US 013760); Banilad, Dumaguete, Negros Oriental, 3 Jun 1978, leg. SIPHILEXP-78 (US 088530); Calindagan Reef, Dumaguete City, Negros Oriental, 6 Jun 1978, leg. SIPHILEXP-78 (US 088531); Malo, Siaton, Negros Oriental, 14 May 1979, leg. SIPHILEXP-79 (US 088533); Magnesia Virae, Catanduanes, 15 Oct. 1980, leg. P. A. Cordero and Tuangpalan (US 091394).
- Indonesia: Cape Batu Kerapo, Salayer, 06 Sept. 84, leg. Snellius-II (L 0108602), 07 Oct. 84 (L 0108603); Bay of Sanggar, Sumbawa, 21/22-Sept. 84, leg. Snellius-II (L 0108601).
- Australia: Heron Island QLD, 10 Aug. 1988, leg. A. B. Cribb (SAP 051714); Jurien Bay WA, 1997, leg. J. Huisman (CWC 1997, R127); Tantabiddi, Ningaloo, 24 April 1996, leg. J. Huisman, (MURU, NR 248); Eagles Nest, Barrow Island, 26 Nov. 1995, leg. J. Huisman (MURU, B262); Ti Tree, Barrow Island, 24 Nov. 1995, leg. J. Huisman (MURU, B79); Montebello Islands, 10 July 1992, leg. J. Huisman (MURU, JH240).

- Mauritius: *Delesseria rhodantha* Harvey (holotype) (= *Amansia rhodantha*): Cap Malheureux, Mauritius, in TCD (Telfair, 1834); *Amansia rhodantha*: n.d., leg. M de Robillard (L 0108599); n.d., leg. W. G. Farlow (L 0108597); n.d., leg. anon. (US 02890).
- Mozambique: Ponta Abril, Inhaca Peninsula, 30 Jun. 1954, leg. W. E. Isaac (L 0108594).
- Kenya: Mombassa, Jul. 1876, leg. J. M. Hildebrandt (L 0108600); Diani Beach, Bahati, 17 Mar. 1965, leg. W. E. Isaac (L 0108595).

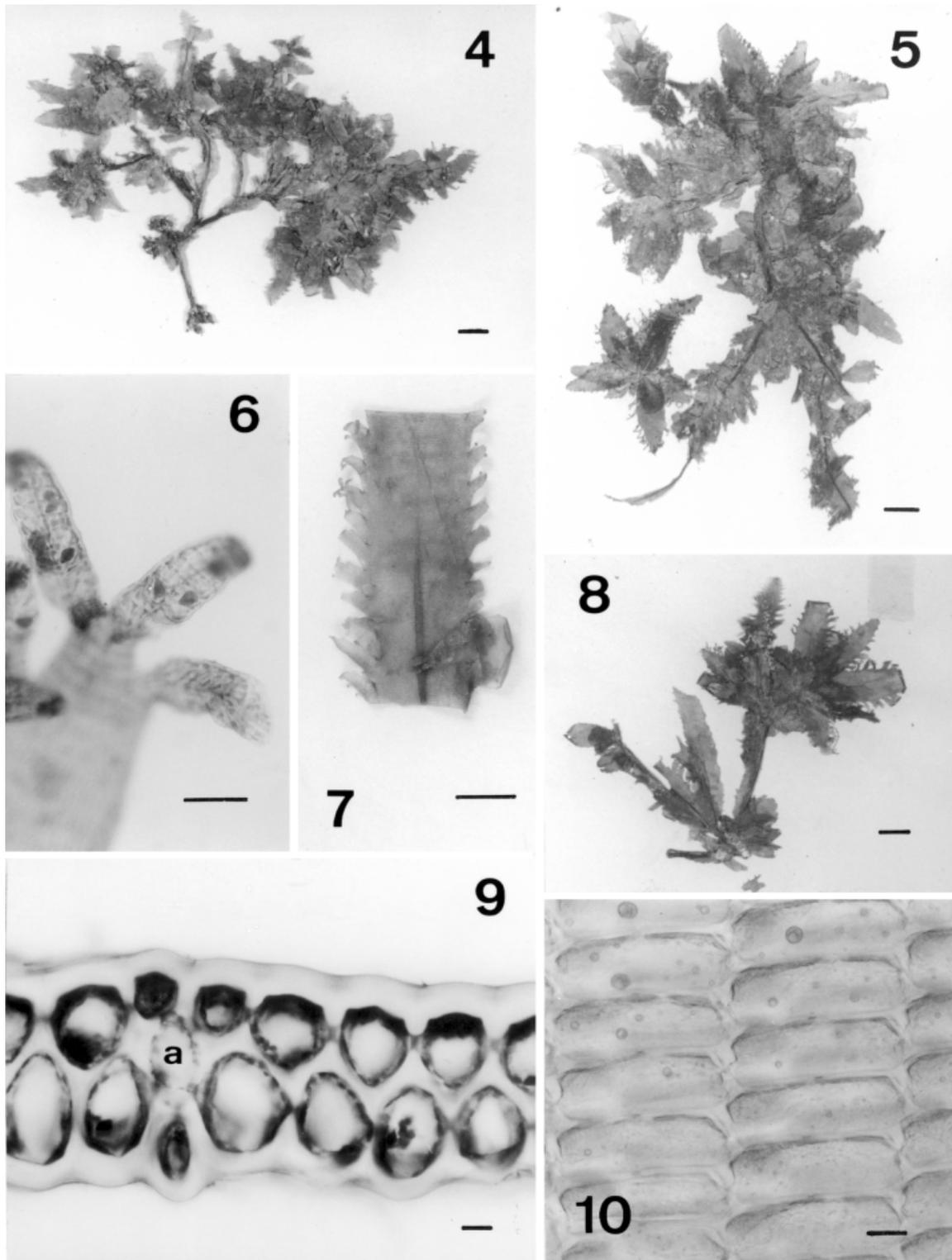
Melanamansia glomerata

- Hawaiian Islands: Hawaiian Islands, c. 1819, leg. C. Gaudichaud ('*Amansia glomerata*', Lectotype, LD 42600 / 0772); Hanauma Bay Beach Park, Oahu, 5 June 1967, leg. M. Littler (US 163490); Kipukai, Kauai, 9 Sept. 1979, leg. W. H. Magruder (US 086459); Lawai Kai, Kauai, 27 Dec. 1979, leg. G. Daida (US 086755); Hakula, Oahu, 16 Nov. 1984, leg. M. Cannon (SAP 052062); Oahu, 16 March 1991, leg. G. R. South (SUVA-A 5431).
- Fiji: 'Feejee', 1838–42, leg. Wilkes Exploring Expedition (US 04057b) (doubtful record; see text).
- Lord Howe Island: 18 Aug. 1981, leg. G. R. South (SUVA-A 5544; *fide* G. R. South in lit.).
- New Caledonia: Lajeu Sudouest, n.d., leg. B. Richer de Forges (AL 288d-CG 77a); Unia, 1983, leg. Plongeurs IRD (AL 288a, AL 288b).
- Philippines: Actin, Basay, Negros Oriental, 29 May 1978, leg. SIPHILEXP-78 (US 088532); Potipot Is., Candelaria Zambales, 28 Nov. 1980, leg. P. A. Cordero and Tuangpalan (US 091395).
- Kenya: Mombassa, Jul. 1876, leg. J. M. Hildebrandt (L 0108596, L 0108598).

Table I presents the average results of morphological measurements carried out on *Amansia rhodantha*, *A. paloloensis* and *Melanamansia glomerata* specimens examined in this study.

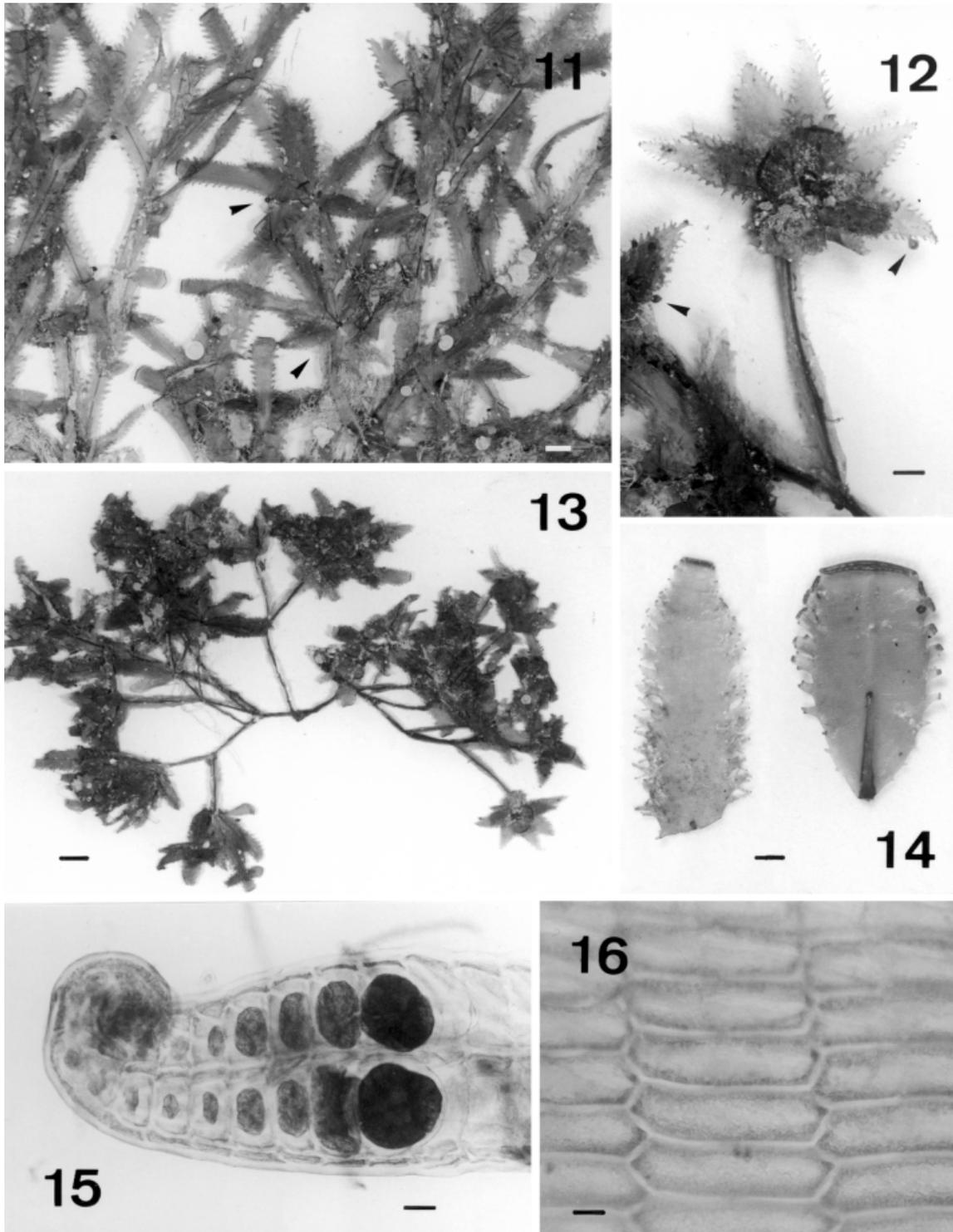
Taxonomic results

Amansia rhodantha (Harvey) J. Agardh 1841: 26; R. E. Norris 1988b: 211, figs 1–11 (as *Amansia glomerata* C. Agardh); Silva *et al.* 1996: 472; Masuda *et al.* 2000: 188, figs 37–42. **Figs 4–10**



Figs 4–10. *Amansia rhodantha*.

Figs 4, 5, 8. Habit of mature plant from the type locality, Mauritius, Indian Ocean, showing both lax and dense growth forms. US 02890 (scale bars = 3 mm). Fig. 6. Detail of tetrasporangial stichidia on lateral endogenous branch. Type material of *Delesseria rhodantha* Harvey, in TCD (scale bar = 200 μ m). Fig. 7. Secondary branchlet, showing marginal serrations, and a pair of budding branchlets from the midrib in the lower half. Rehydrated type material of *Delesseria rhodantha* Harvey, in TCD (scale bar = 2.5 mm). Fig. 9. Axial structure of blade, showing axial cell (a) surrounded by five pericentral cells. SUVA-A 5437L, from Rotuma Island, South Pacific (scale bar = 10 μ m). Fig. 10. Surface view of segment cells of blade alae. Type material of *Delesseria rhodantha* Harvey, in TCD (scale bar = 25 μ m).



Figs 11–16. *Amansia paloloensis* from Samoa.

Fig. 11. Detail of the holotype (SUVA-A 1565), showing both lax branching and the presence of rosettes (arrowheads) (scale bar = 4 mm). Fig. 12. Detail of morphologically distinct mature rosette and corticated axis. Note marginal cystocarps (arrowheads). SUVA-A 3892 (scale bar = 2.5 mm). Fig. 13. Habit of mature plant, with numerous rosette axes. Compare with Fig. 4. SUVA-A 3892 (scale bar = 12 mm). Fig. 14. Detail of blades, showing lateral endogenous branches and midrib. SUVA-A 5479L (scale bar = 1 mm). Fig. 15. Tetrasporangial stichidia of *Amansia rhodantha* from Beqa, Fiji. SUVA-A 5436L (scale bar = 50 μ m). Fig. 16. Segment cells of blade alae in surface view. Holotype of *Amansia paloloensis*, SUVA-A 1565 (scale bar = 25 μ m).

Basionym: *Delesseria rhodantha* Harvey 1834: 151–152, plate CXXVI, figs 1–3 (type locality: Cap Malheureux, Mauritius; holotype in TCD, Dublin).

Synonymy: *Rytiphlaea rhodantha* (Harvey) Decaisne 1842: 358. *Amansia paloloensis* South et Skelton 1999: 247, figs 2–14 (type locality: Palolo Deep Marine Reserve, Apia, Samoa). **Figs 11–16**

Misapplied names: *Amansia glomerata* C. Agardh 1824: 194; Weber-van Bosse 1923: 369; Okamura 1900: 71, pl. XXV, figs 1–13; Falkenberg 1901: 416, pl. 1, figs 19–21, pl. 6, figs 14–29; Yamada and Tanaka 1938: 86; Fritsch 1945: 570, fig. 212a, e–i; Isaac 1956: 188, fig. 20; Isaac and Isaac 1968: 24, pl. 4B; Kylin 1956: 544, fig. 436B; Womersley and Bailey 1970: 336; Jaasund 1976: 131, fig. 267; Tsuda and Wray 1977: 103; Cribb 1983: 106, pl. 31 fig. 1; Payri and Meinesz 1985: 511; Lewis and Norris 1987: 22; Silva *et al.* 1987: 61; Garrigue and Tsuda 1988: 63; Norris 1988b: 211, figs 1–11. – *Melanamansia glomerata* (C. Agardh) R. E. Norris 1995: 67; Yoshida *et al.* 1995: 150; N'Yeurt 1996: 428, figs 127, 128, 185, 197, 198; N'Yeurt *et al.* 1996: 87; Payri and N'Yeurt 1997: 897; Millar 1999: 523 (unverified record); Millar *et al.* 1999: 573, fig. 6E (unverified record); Coppejans and Millar 2000: 333 (unverified record).

Distribution: Tropical Indian Ocean, South-East Asia, Japan, Tropical Pacific Ocean.

The thallus is rose-red, up to 100 (on average 40) mm high. Branching is lax to profuse and usually forms deep-red leafy rosettes of secondary branchlets when fully mature. Secondary blades develop as successive pairs on the dorsal side of the midrib, and are crisp and lanceolate, up to 35 mm long and 6 mm broad, 85–110 μm thick, with more or less pronounced marginal serrations 1–4 mm long (which represent endogenous branches) always present. A distinct midrib up to 1 mm wide is present in the lower half of ultimate branchlets, and the apex is characteristically in-rolled. The number of segments between alternating veins (determinate branches covered by the corticating pericentral cell derivatives; Norris 1995: 66) is usually 4, with a range of 1–5. Deciduous, colourless and uniseriate dorsal trichoblasts up to 8 cells long develop on every second or third axial cell (or on every segment in determinate marginal branchlets), and are initially vesiculate. The main axis is irregularly branched, stem-like and rigid in basal portions, to

0.8 mm in diameter. Internal structure is cellular, with a central axial cell 28–30 μm in diameter surrounded by five pericentral cells 36–40 μm in diameter (Figs 1, 2, 9), and two displaced rows of regularly arranged hexagonal alar cells 20–29 \times 92–129 μm in surface view. Tetrasporangia occur in flattened, pinnately arranged marginal stichidia up to 340 μm long and 290 μm in diameter. Individual tetrasporangia are spherical and tetrahedrally divided, 100–112 μm in diameter, in up to 10 regularly disposed pairs. Procarps and curved spermatangial heads are 200–450 μm in diameter and are dorsal on the involucre tips of endogenous lateral branches, while cystocarps 700–1000 μm in diameter occur usually singly and terminally on endogenous branches. Carposporangia are lanceolate, 25–42 \times 83–125 μm .

Melanamansia glomerata (C. Agardh) R. E. Norris 1995: 67; Abbott 1999: 404, fig. 118C–J. **Figs 17–24**

Basionym: *Amansia glomerata* C. Agardh 1824: 247.

Known distribution: Hawaiian Islands, Philippines, Vietnam, Fiji, New Caledonia, Kenya.

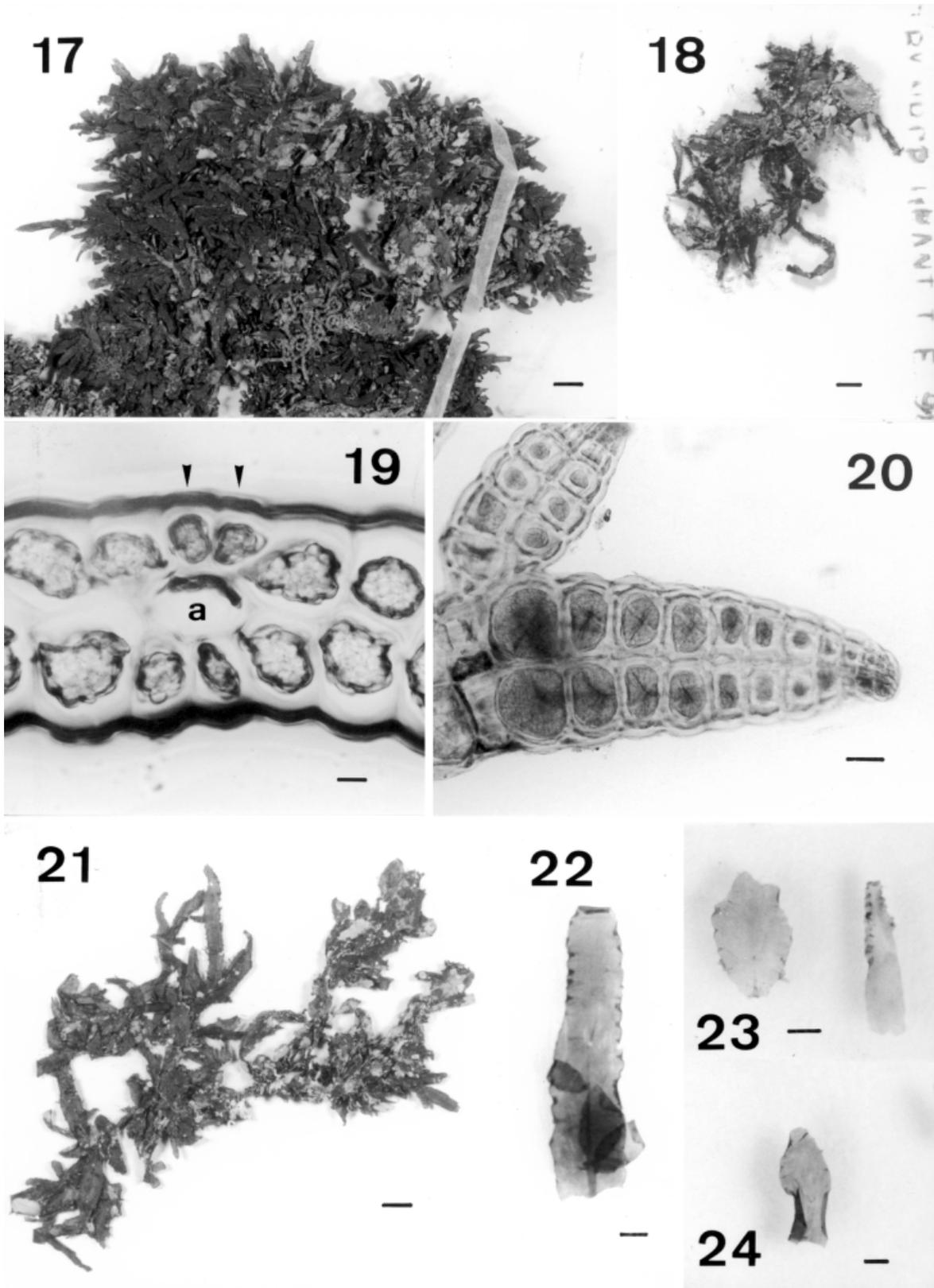
Plants are brownish-red, on average 53 mm high, and are composed of lanceolate to ovate blades to 100 mm long and 3 mm wide, with in-rolled leaf apex. Blade margins are smooth, or with regular serrations (endogenous branches). A central midrib is present, becoming narrower and disappearing towards the apex. The number of segments between alternating veins (determinate branches covered by the corticating pericentral cell derivatives; Norris 1995: 66) is on average 4.4, with a range of 3–6. Trichoblasts are sparse, they are up to 4 cells long and non-vesiculate. The central axial cell is 28–30 μm in diameter, surrounded by five pericentral cells, with the first two dorsal pericentral cells each developing a smaller pseudo-pericentral cell 13.8–14.5 μm in diameter that lies adjacent to the axial cell (Figs 3, 19). The stem of plants is thick and cartilaginous, 0.5–0.7 mm broad, denuded below. Ultimate branchlets are ecorticate, 77–110 μm thick, composed of two overlapping layers of elongate hexagonal cells in transverse rows; each cell is about 20–20 \times 87–100 μm in surface view. Marginal teeth are up to 1 mm long and 445 μm broad. Tetrasporangial stichidia are pinnately arranged on either side of blade margins, up to 750 μm long and 250 μm broad, containing up to 10

Figs 17–24. *Melanamansia glomerata*.

Fig. 17. Plant from Mombassa, Kenya, East Africa. L 0108598 (scale bar = 5 mm). Fig. 18. Plant from Potipot Island, Philippines. US 091395 (scale bar = 5 mm). Fig. 19. Axial structure of plant from Lajeu, New Caledonia, showing pseudo-pericentral cells (arrowheads) surrounding (but not directly connected to) axial cell (a). CG77a (scale bar = 10 μm). Fig. 20. Tetrasporangial stichidia of plant from Oahu. Note that the stichidia is twice laterally branched. SUVA-A 5431 (scale bar = 50 μm). Fig. 21. Plant from Unia, New Caledonia. AL288b (scale bar = 5 mm). Fig. 22. Detail of blade of plant from Mombassa, Kenya, showing smooth margins and elongate shape. L 0108598 (scale bar = 700 μm). Fig. 23. Blades of plant assumed to be from the Fiji Islands (see text). US 4057b (scale bar = 1 mm). Fig. 24. Blade of plant from Lajeu, New Caledonia. CG77a (scale bar = 1 mm).

pairs of tetrahedrally-divided tetrasporangia which are 50–100 μm in diameter. Spermatangial heads are curved and arranged in marginal clusters; procarps and cystocarps occur on endogenous marginal

branches. In all cases, the colour of the *Melanamansia* plants was noticeably brownish-red, and stained the herbarium mounting paper.



Discussion

The holotype of *Delesseria rhodantha* Harvey

An examination by the author of a rehydrated blade fragment of the holotype of *Delesseria rhodantha* Harvey in TCD (Fig. 7) shows features similar to those seen in blades of South Pacific material previously ascribed to *Amansia glomerata*, and a cross section of the blade clearly shows the five pericentral cells around the axial ring, and absence of pseudo-pericentral cells. The habit and description of the holotype by Harvey (1834: 151, plate CXXVI, figs 1–4) indicate features quite similar to those found in the *Amansia* species considered in this study from localities in both the Indian Ocean and the tropical Pacific Ocean, including the presence of both tight and lax rosettes of secondary branches and alar cells on the primary axes. On the other hand, a re-examination of the lectotype of *Amansia glomerata* C. Agardh from Hawaii (LD 42600 / 0772) clearly shows the presence of paired dorsal pseudo-pericentral cells in a blade cross section (Fig. 3) which distinguishes that plant from *A. rhodantha*. On the basis of these observations, material from the Tropical Pacific and Indian Oceans previously known as *Amansia glomerata* (or misidentified as *Melanamansia glomerata*, when pseudo-pericentral cells were found to be absent) are considered conspecific with *Amansia rhodantha*.

The status of *Amansia paloloensis* South et Skelton

South and Skelton (1999) described a new species of *Amansia* from Samoa, and these authors considered the lack of highly corticated axes, the absence of blades organized in morphologically distinct tight axes around the parent axis, and a weakly developed midrib as characters distinguishing *A. paloloensis* from *A. rhodantha* as described and illustrated by Norris (1988b: 211). The drawing of the holotype (South and Skelton 1999: 246, fig. 2) indeed shows a plant with loriform, serrate branches and lax 'rosettes' of secondary blades issued from the weakly developed midrib. The present author has re-examined the holotype, isotype and other collections of *A. paloloensis* from the type locality, and found a significant number of thalli with morphologically distinct primary corticated axes and relatively tight and lax rosettes of secondary blades on rosette axes (Figs 11,13). These plants also had blades with well-developed midribs in the lower half (Fig. 14) and corticated rosette axes (Fig. 12), indicating that the morphology of the species is influenced perhaps by environmental factors. More importantly, a comparison of material of *A. rhodantha* from the type collection and localities in Mauritius, Kenya, Mozambique and Western Australia, as well as *Amansia* species from Taiwan, Japan, the Philippines, Eastern Australia, New Caledonia, Fiji, Rotuma, the Cook Islands

and French Polynesia (Table I) with *A. paloloensis* showed no major difference in the range of characteristics among them. Characters such as the degree of rosette formation, length of the blades, degree of cortication of the midrib and position of the reproductive stichidia are equally quite variable in plants from the same and similar populations, with for instance *A. rhodantha* from Western Australia (MURU B262; MURU 248), having tight rosettes as well as very lax, loriform blades reminiscent of some specimens of *A. paloloensis*. The reproductive and trichoblast anatomy of *A. paloloensis*, which is well-documented and illustrated in the protologue of the species, is comparable to *A. rhodantha* (South and Skelton 1999: 249). Now that the Samoan species has been compared with genuine herbarium material of *A. rhodantha* from the Indian Ocean and other localities, it appears to be conspecific with the latter species and thus extends the status of *A. rhodantha* as a pan-tropical entity.

Melanamansia glomerata in the tropical Pacific

Wilson and Kraft (2000: 366) commented that the generic segregation of *Melanamansia* from *Amansia* is probably not warranted, since the presence of pseudo-pericentral cells is an inconsistent attribute in species of *Neurymenia*, *Vidalia*, *Kuetzingia*, and *Ceramium*. However, additional distinguishing characteristics of *Melanamansia* are a darkly coloured brown thallus which stains the mounting paper when dried (possibly linked to differences in chemical composition; M. Masuda pers. com.), regularly alternate marginal serrations which are not as pronounced as in *Amansia rhodantha* and which are often absent; generally smaller, thicker, more coriaceous branchlets with less apparent midribs (this study); and trichoblasts lacking protective vesicles when young (Norris 1988b). From this study, an additional field test to distinguish *Amansia* spp. from *Melanamansia glomerata* was found: when preserved in 4% Formalin-seawater and exposed to ambient light for several days, *Amansia* tends to bleach to translucent white, while *Melanamansia* becomes dark brown, apparently because the brown pigments (presumably polyphenols) are less susceptible to the bleaching action of the preservative (as is the case in species of brown algae such as *Sargassum* and *Turbinaria*).

In the Fiji Islands, a single record for this genus exists (collected from 'Feejee' by the Charles Wilkes U.S. Exploring Expedition, between 1838 and 1842 (US 04057b, Fig. 23) but the plant has not been collected in Fiji waters since. The Wilkes collection consists of two plants, one of which (US 04057a) is *Amansia rhodantha*, while the other (US 04057b) is *Melanamansia glomerata*. While there is no doubt as to the generic identity of the latter specimen, Smith (1979: 38–40) points out that the accounting and

recording of the Wilkes Expedition collections was not very satisfactory, and hence the precise locality and date of this *Melanamansia* collection from Fiji is unknown. There is a possibility it might have been mixed with collections from neighbouring localities such as the Solomon Islands. The author has unsuccessfully tried to obtain material from the latter locality, so it cannot be confirmed at this stage if *M. glomerata* occurs in the Solomon Islands. However, in some cases, *M. glomerata* occurs in the same habitat as *Amansia rhodantha* (e.g. in New Caledonia and Kenya), adding to the confusion between the two genera. *Melanamansia glomerata* is unlikely to be confused with other *Melanamansia* species because of its unique combination of characteristics (Norris 1988b; 1995).

Validity of current criteria to distinguish the Amansieae

Characters that have proved useful in distinguishing species in the Amansieae include the presence or absence of pseudo-pericentral cells, the vesiculate (in *Amansia*) or non-vesiculate (in *Melanamansia*) nature of trichoblasts, degree of marginal serrations and thallus flattening, type of endogenous branching, the presence or absence of bladelets in rosettes, position of the reproductive axes and the distinctness of the axial ring in rosette axes (Norris 1988a, Wilson and Kraft 2000).

Herbarium and liquid-preserved samples of *Amansia* and *Melanamansia* species from the Pacific, Indonesian and Indian Ocean region were sectioned and examined for pseudo-pericentral cells. In most instances, except the Hawaiian samples, and some samples from Kenya, the Philippines, Fiji and New Caledonia (Table I), pseudo-pericentral cells were universally absent. Herbarium specimens of '*Amansia glomerata*' from southern Japan housed in SAP (Hokkaido University) were examined, and found to consistently lack pseudo-pericentral cells and a similar observation was made on samples from Taiwan. When pseudo-pericentral cells were present, they were clearly apparent and about half the size of pericentral cells (Fig. 19). Fijian and French Polynesian specimens previously ascribed to *Melanamansia* (N'Yeurt *et al.* 1996, Payri and N'Yeurt 1997) were re-examined, and found to lack pseudo-pericentral cells, thus placing them in *Amansia*. Indian Ocean *Amansia rhodantha* also lacked such cells, while in Malaysia Masuda *et al.* (2000: 188, fig. 41) similarly report the absence of pseudo-pericentral cells in *A. rhodantha*. The presence or absence of these pseudo-pericentral cells hence appears to be a good generic criterion, and is backed by other morphological and biochemical differences (Norris 1988b, M. Masuda, pers. com.).

All *Amansia rhodantha* specimens examined had fairly prominent, alternate marginal proliferations (which represent non-determinate or endogenous

secondary branchlets) 2–5 mm long (Fig. 7). In *Melanamansia glomerata* these marginal serrations were much less pronounced (but more regular than in *Amansia rhodantha*, when present), and in some instances lacking altogether, with the blades smooth and superficially reminiscent of those of some *Sargassum* species (Figs 22–24).

Proliferations from the ventral midrib (aside from secondary branchlets) were only found to be abundant in some of the Indonesian *Amansia rhodantha* specimens from Salayer (e.g. L 0108603), which also had a consistently thicker thallus. These ventral, irregularly dichotomous proliferations lack alar cells, and would seem to function as attachment haptera, perhaps an adaptation to the exposed habitats where the plants came from.

From an examination of the specimens at hand, it was observed that rosettes of blades along the secondary axes, which is a characteristic feature of both *Amansia* and *Melanamansia* (Norris 1988b) can vary from lax to tight, both on the same plant and within individuals in similar populations. Generally, older plants tend to have thicker, more corticated secondary and primary axes with tight rosettes, while younger plants have less cortication and more lax or absent rosettes of blades. Also, environmental factors seem to play a role in determining the degree of rosette formation. For instance, in the case of *A. paloloensis*, the description of the species states that branches have the same shape as the main axis (i.e. both have an ala) and are arranged in 'lax' rosettes (South and Skelton 1999: 247, fig. 2), which was the main reason for separating the species from *A. rhodantha*. However, an examination of the holotype and liquid-preserved and pressed isotypes of *A. paloloensis* revealed a wide range in the degree of rosette formations and cortication of the secondary axes and presence of alae on primary axes, and the presence of tight and lax rosettes of secondary branches on the same plant (Figs 11–13). Indeed, some specimens were virtually indistinguishable from specimens of *A. rhodantha* from Mauritius and Western Australia (compare Figs 4, 5, 13). The illustration by Harvey of the holotype of *Delesseria rhodantha* (1834, pl. CXXVI, fig. 1) shows both the presence of tight and lax rosettes of secondary branches, and a main axis with alar cells not very distinct from secondary branches. It would seem that perhaps shallow, more exposed conditions (such as on fringing reefs) favour tight rosette formation (which is more hydrodynamically resistant) while more lax arrangements are possible in deeper, calm waters (such as blue holes, in the case of *Amansia paloloensis*). Ecological studies would be needed to verify these hypotheses; however it is clear that the degree of rosette formation and cortication of the axes is not a reliable taxonomic character at the species level in *Amansia*.

Norris (1988b: 211) reported that rosette axes in

Amansia from Natal have an ill-defined axial row of cells. This feature was examined on a range of specimens of *Amansia* from the South Pacific and the Indian Ocean but no significant difference was seen in these specimens, as the axial ring was still discernible in all sections made, only being more or less surrounded by cortication. This also varied according to the degree of rosette formation and age of the plant. Hence the distinctness of the axial ring was not found a reliable taxonomic character among the species examined.

Tetrasporangial stichidia are basically similar in both *Amansia rhodantha* and *Melanamansia glomerata*, in that they are typically rhodomelaceous with pairs of tetrasporangia in up to ten rows, in elongate flattened and pinnate stichidia which are usually on lateral marginal branchlets, but can also occur apically. Cover cells usually totally cover the developing sporangia. One feature which was noted in *Melanamansia glomerata* is that individual tetrasporangial stichidia are often laterally branched once or twice (Fig. 20), which was not seen in *Amansia rhodantha* (Figs 6, 15).

Cells of the blade alae in both *Amansia* and *Melanamansia* are regularly elongate-hexagonal, and occur in two overlapping and slightly offset layers radiating on either side of the midrib. An examination of these elegant cells in species of *Amansia* (Figs 10, 16) and *Melanamansia* show no particular difference, with the length of segments ranging from 80 to 120 μm . However, it was noted that in *Melanamansia* the range was more restricted, with most specimens having segment lengths of about 100 μm , which was

also recorded by Norris (1988b) for Hawaiian material.

An additional potentially useful character is the number of segments between lateral 'veins' on the blades, which are in fact determinate branches covered by the pericentral cell derivatives. These can be easily detected in the unrolled apical portions of the blades by the developing trichoblast terminating each such alternating 'vein' (Norris 1995 and pers. com.). Norris (1995: 66) counted the number of segment cells between these alternating veins for several species of *Melanamansia* and *Amansia*, and found them relatively constant. In *A. rhodantha* specimens observed in this study, the number ranged from 3 to 7, usually 3 or 4 with an average of 3.3. In *Melanamansia* it averages 4.4 (Norris 1995), but the range is reportedly less than in *Amansia rhodantha*. At this stage there seems to be no largely significant difference in the number of segments between alternating veins in the specimens of *A. rhodantha* studied.

From Table I, a number of preliminary conclusions can be made: A. There appears to be no notable difference in the range of thallus size, blade dimensions, cortication of axes and rosette formation between specimens of *Amansia rhodantha* studied, as well as between *A. rhodantha* and *A. paloloensis*. B. *Melanamansia glomerata* from all localities studied have consistently smoother, smaller and narrower blades, as well as more corticated axes. These differences reinforce the conspecificity of the *Amansia rhodantha* and *A. paloloensis* specimens studied, as well as the generic distinctness of *Melanamansia glomerata*.

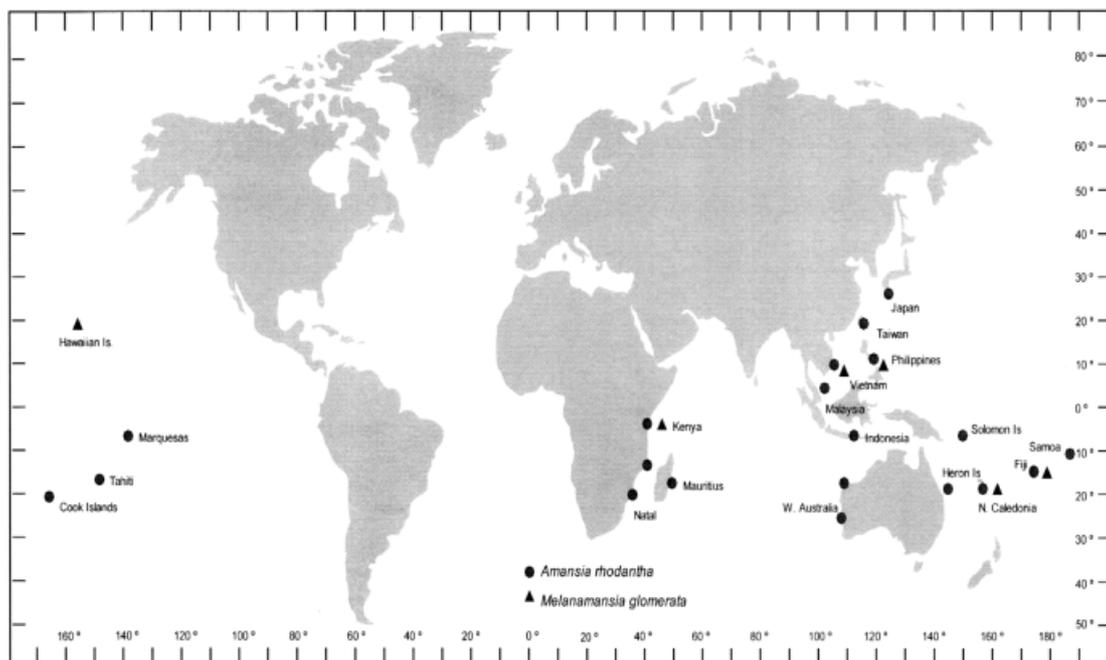


Fig. 25. Biogeographical map for *Amansia rhodantha* (circle) and *Melanamansia glomerata* (triangle), showing the currently known distribution.

Conclusions

The results of this study and those of South and Skelton (1999) and of Masuda *et al.* (2000) confirm that the genus *Amansia* does exist in the Pacific Ocean, and it appears that *Melanamansia glomerata* is so far restricted to Hawaii (Norris 1995), New Caledonia and the Philippines (this study), Lord Howe Island (G. R. South pers. com.), Vietnam and Malaysia (M. Masuda pers. com.), Kenya (this study), and possibly other localities which are not yet adequately investigated. It is clear that both *A. rhodantha* and *Melanamansia glomerata* are more widely distributed than previously thought, and each genus is consistently differentiated from the other by a number of anatomical and biochemical characters. Figure 25 presents a world distribution of these two genera as it is currently known.

Revised Key to the Species of *Amansia* and *Melanamansia* in the South Pacific

- Presence of paired dorsal pericentral cells; pigments reddish-brown; trichoblasts non-vesiculate, sparse, composed of up to 4 cells: *Melanamansia glomerata*;
- Absence of paired dorsal pericentral cells; pig-

ments rose-red; trichoblasts on every second or third axial cell, initially vesiculate and composed of up to 8 cells: *Amansia rhodantha*.

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