

A re-assessment of the species previously included in *Lenormandiopsis* including the description of *Aneurianna* gen. nov. (Rhodomelaceae, Ceramiales)

Louise E. PHILLIPS*

*School of Biological Sciences, Monash University, Clayton,
Victoria 3800, Australia*

(Received 15 February 2006, Accepted 21 March 2006)

Abstract – The genus *Lenormandiopsis* is a member of the tribe Amansieae characterised by broad foliar blades. In a recent study it was established that the type species of *Lenormandiopsis*, *L. latifolia*, conformed to the generic characteristics of the genus *Lenormandia*, to which it was returned, effectively subsuming the genus *Lenormandiopsis* within *Lenormandia*. In the current study, the morphology and anatomy of the remaining species of the former *Lenormandiopsis* have been examined and found not to share the characteristics of *Lenormandia*. A new genus, *Aneurianna*, is established for them, with *A. lorentzii* as the type species, *A. nozawae* and the newly described *A. dentata*. *Lenormandiopsis parthasarathyi* is found to be conspecific with *A. lorentzii*. The new genus is distinguished from the remainder of the Amansieae by the foliar blades and endogenous branching, and also by the surface pattern of irregular ellipses.

Amansieae / Ceramiales / *Aneurianna* / *Lenormandiopsis* / morphology / Rhodomelaceae / Rhodophyta / systematics / taxonomy

Résumé – Réévaluation des espèces précédemment dans le genre *Lenormandiopsis* et description d'*Aneurianna* gen. nov. (Rhodomelaceae, Rhodophyta). Le genre *Lenormandiopsis* appartient à la tribu des Amansieae caractérisée par de larges lames foliaires. Il a été établi récemment que l'espèce type du *Lenormandiopsis*, *L. latifolia*, correspond aux caractères génériques du genre *Lenormandia*, dans lequel elle a été remplacée, *Lenormandiopsis* devenant un synonyme de *Lenormandia*. Dans la présente étude, la morphologie et l'anatomie des espèces restant dans le précédent *Lenormandiopsis* ont été examinées : ces espèces ne partagent pas les caractéristiques du *Lenormandia*. Il a été établi un nouveau genre pour ces espèces : *Aneurianna*, comprenant *A. lorentzii* comme espèce type, *A. nozawae* et la nouvelle espèce *A. dentata*. *Lenormandiopsis parthasarathyi* est conspécifique avec *A. lorentzii*. Le nouveau genre se distingue des autres Amansieae par les lames foliaires, une ramification endogène, et aussi par des aréolations elliptiques irrégulières à la surface des lames.

Amansieae / Ceramiales / *Aneurianna* / *Lenormandiopsis* / morphologie / Rhodomelaceae / Rhodophyta / systématique / taxonomie

* Correspondence and reprints: wheeze_phillips@hotmail.com
Communicating editor: John Huisman

INTRODUCTION

Lenormandiopsis Papenfuss was a genus of four species belonging to the rhodomelacean tribe Amansieae. In a recent study of the genus *Lenormandia* Sonder (Phillips, 2002), it was shown that the type species of *Lenormandiopsis*, *L. latifolia* (Harvey et Greville) Papenfuss, conforms in key aspects of vegetative and reproductive morphology, as well as 18S rDNA sequences, to the remainder of *Lenormandia sensu stricto*. When *Lenormandiopsis latifolia* was returned to *Lenormandia*, *Lenormandiopsis* became a synonym of *Lenormandia*. The remaining species of the former *Lenormandiopsis* do not, however, fit the generic circumscription of *Lenormandia*, and their characteristics and generic placement are the subject of this study.

The genus name *Lenormandiopsis* was a substitution, for the name *Aneuria* (J.Agardh) Weber-van Bosse, made by Papenfuss (1967) after consultation with the General Committee of the International Botanical Congress, who judged the latter to be a later homonym of the liverwort genus *Aneura* Dumortier (1822). Weber-van Bosse first used the name *Aneuria* at the generic rank in 1911, when she described a new species, *A. lorentzii*, from Thursday Island, East Timor and Borneo. It may be that Weber-van Bosse's (1911) intention was to base the genus on *A. lorentzii*, as she did not mention any other species. However, in establishing the genus, Weber-van Bosse made explicit reference to the sub-genus *Aneuria* of *Lenormandia*, which had been created in 1892 by J. Agardh based on *Lenormandia latifolia* Harvey et Greville from Western Australia. Weber-van Bosse (1911, p. 30-31) noted that because the genus was an elevation of the earlier sub-genus of the same name, its authorship should be recognised as *Aneuria* (J.Agardh) Weber-van Bosse. The implication of this, recognised by Papenfuss (1967), was that the type species of the sub-genus *Aneuria* must be recognised as the generitype. The only species included in J. Agardh's (1892) sub-genus *Aneuria* was *Lenormandia latifolia*, which was not validly transferred to *Aneuria* until more than ten years later (De Toni, 1924).

Weber-van Bosse's (1911) original description of *Aneuria* refers to flat fronds membranaceous to coriaceous in texture, with entire margins, reflexed apices, endogenous branches and adventitious reproductive organs. The main justification for separating *Aneuria* from *Lenormandia* was the presence of endogenous branching. These features do not describe the type species [*Aneuria* (*Lenormandiopsis*) *latifolia*], however, which lacks endogenous branching and has flat, cleft apices, further attesting that Weber-van Bosse was, in fact, basing her concept of the genus on *A. lorentzii*.

The distributional range of *A. lorentzii* [now *Lenormandiopsis lorentzii* (Weber-van Bosse) Papenfuss] currently extends from Japan (Okamura, 1929-1932; Nozawa, 1965) south to the Philippines (Kraft *et al.*, 1999), tropical-eastern Australia (Millar & Kraft, 1993) and Natal, South Africa (Norris, 1987a,b). While she described tetrasporangial plants, Weber-van Bosse (1911, 1923) had no collections of gametophytes, females of the species being first described by Nozawa (1965). Male gametophytes have not yet been reported.

Aneuria parthasarathii V.Krishnamurthy was described from India (Krishnamurthy 1967) [= *Lenormandiopsis parthasarathyi* (V.Krishnamurthy) V.Krishnamurthy et H.Joshi (1970)]. Krishnamurthy collected his specimens from the lower intertidal in southern India and had both male and female gametophytes as well as tetrasporic plants. This species was said to differ from *A. lorentzii* mainly in the size of the thallus (smaller in *A. parthasarathyi*) and in

being mostly unbranched, although arrested branches occurred at the margins in the form of lobes, and blades were coriaceous to cartilaginous.

The most recently described species, *L. nozawae* R.E.Norris, was initially based on sterile collections from Natal in South Africa (Norris, 1987a), reproductive material being described separately (Norris, 1987b). *Lenormandiopsis nozawae* was found in deep water (47-56 metres depth) and was considered by Norris to differ from *L. lorentzii* in the length of the tetrasporangial stichidia and in the crenate or coarsely sinuous rather than smooth profile to the margin. Unfortunately, Norris (1987a) only had access to one putative specimen of *L. lorentzii*, also collected from Natal, upon which he based his comparison. Norris (1987a, b) illustrated some of the differences between *L. latifolia* and the other species but did not comment upon these, nor did he discuss differences between *Lenormandiopsis* and *Lenormandia*, despite the fact that the type species of *Lenormandiopsis* was originally included in that genus.

An examination of the type species of *Lenormandiopsis*, *L. latifolia*, (Phillips, 2002) showed clearly that it belonged to the genus *Lenormandia*. The detailed morphological investigation of the remaining species of *Lenormandiopsis* presented here shows that they do not conform to the generic characteristics of *Lenormandia* and are rightly considered as belonging to their own separate genus. The new genus is similar in concept to that originally proposed by Weber-van Bosse for *Aneuria* based, presumably, on *A. lorentzii*, which serves as the type species for *Aneurianna* gen. nov.

MATERIALS AND METHODS

Anatomical observations were made from herbarium specimens. Sections were cut by hand with a single-edged razor blade, rehydrated in a weak detergent solution, stained in 1% acidified aniline-blue solution, and mounted on glass slides in 20%-50% Karo™ corn syrup (CPC International Inc., Englewood Cliff, NJ).

Herbarium specimens were scanned using a UMAX Astra 2100s flatbed scanner (Umax Systems GmbH, Willich, Germany), low-power habit micrographs were photographed using a WILD photoautomat MPS 55 macroscope (Leica, Heidelberg, Germany), and photomicrographs were taken on ZEISS Axioskop2 microscope (Carl Zeiss, Oberkochen, Germany).

Sequences of the 18S rRNA gene were obtained following the methods described in Phillips *et al.* (2000) for the following species: *Aneurianna dentata* (Jurien Bay, Western Australia, 1.2 metres depth, *Huisman*, 26 Oct 2000, MURU JB673, Genbank accession number AY237280), *Lenormandia marginata* Hook.f. et Harv. (East Cape, Cape Conran, Victoria, drift, *Sjerp*, 2 Jan 2001, LEP 61-1, Genbank accession number AY237281) and *Polysiphonia howei* Hollenberg (Talisoy, Vivac Catanduanes, Philippines, *West*, 14 May 1988, JAW 2922, Genbank accession number AY237282). Using SeqPup (Gilbert, 1995), the sequences were added by eye to an alignment of 11 previously published species (Table 1).

The alignment was converted into an unordered character state matrix using the PAUP computer package version 4.0b2a (Swofford, 1999). All characters were equally weighted and gaps were treated as missing data. Most-parsimonious trees were obtained using the branch-and-bound search option.

Table 1. Previously published 18S rRNA sequences used in multiple alignment.

<i>Species</i>	<i>Genbank Accession No.</i>
<i>Adamsiella lorata</i> L.E.Phillips <i>et</i> W.A.Nelson	AF339898
<i>Adamsiella melchiori</i> L.E.Phillips <i>et</i> W.A.Nelson	AF339897
<i>Amansia glomerata</i> C. Agardh	AF251512
<i>Epiglossum proliferum</i> (C.Agardh) L.E.Phillips	AF203895
<i>Epiglossum smithiae</i> Hook.f. <i>et</i> Harv.	AF339895
<i>Halopithys incurva</i> (Huds.) Batters	AF251513
<i>Lenormandia latifolia</i> Harv. <i>et</i> Grev.	AF339893
<i>Lenormandia muelleri</i> Sond.	AF203897
<i>Lenormandia pardalis</i> J.Agardh	AF339894
<i>Lenormandia spectabilis</i> Sond.	AF339896
<i>Neurymenia fraxinifolia</i> (Mert. <i>ex</i> Turner) J.Agardh	AF339899
<i>Protokuetzingia australasica</i> (Mont.) Falkenb.	AF339901

Once obtained, trees were rooted with reference to the outgroup species *Polysiphonia howei*. This species was chosen as a clade containing *Polysiphonia* species has been found to be next-most closely related to the Amansieae in previous analyses (Phillips, 2000; Phillips *et al.*, 2000; Phillips, 2001). One thousand bootstrap replicates were performed to obtain a measure of the robustness of the phylogeny.

The maximum likelihood analysis was conducted using a likelihood model estimated from the data set and refined through successive tree searches. The result corresponded to the Hasegawa-Kishino-Yano model (Hasegawa *et al.*, 1985) with a transition/transversion ratio of 2, a proportion of invariable sites estimated as 0.66, with rates (for variable sites) assumed to follow a gamma distribution with shape parameter 0.80. This combination of parameters produced the tree with the highest log-likelihood.

Distance analysis was conducted using the Hasegawa-Kishino-Yano model (Hasegawa *et al.*, 1985); the trees constructed using the neighbour-joining algorithm. One thousand bootstrap replicates of the data set were analysed to assess the robustness of the resultant phylogeny.

RESULTS

Genus *Aneurianna* L.E.Phillips, *gen. nov.*

Aneuria (J.Agardh) Weber-van Bosse, 1911:30-1 (*pro parte*); 1923:371; De Toni, 1924: 428; Kylin, 1956: 548.

non Lenormandia subgenus *Aneuria* J.Agardh, 1892.

Lenormandiopsis Papenfuss, 1967: 102 (*pro parte*); Desikachary *et al.*, 1998: 328.

Genus ad tribum Amansiearum pertinens. Laminae eramosae vel ramis endogenis, late foliaries, erectae, ex haptero discoideo vel hapteroideo orientes; frondes integrae vel lobatae, marginibus integris crenatis dentatisve; costae nullae; trichoblasta vegetativa exogena nulla vel reducta ad cellulam unicam; trichoblasta vegetativa

*adventitia interdum praesentia; cellulae pericentrales 5, pseudopericentrales plerumque 1-4; apices emarginati vel obcordati, in speciebus nonnullis incurvati; medulla e stratis cellularum implexis 2 composita, cellulis a cellulis pericentralibus dorsalibus lateralibusque genitis; cortex e strato unico compositus; superficies laminarum ostendentes ordinationem irregularem areolarum ellipticarum; corticatio secundaria nulla vel tantum in stipite basali vel ad bases laminarum. Stichidia lanceoloidea, in superficiebus laminarum irregulariter disposita et aggregata. Gametophyta dioica, procarpiis epibasalibus in trichoblastis reductis exogenis, e ramulis adventitiis nanis arcuatis irregulariter aggregatis in superficiebus laminarum exorientibus; cystocarpia sessilia globosa. Capitula spermatangialia e segmento sterili unico basali et segmentis fertilibus 3-4 composita, cellula apicali sterili carentia. A *Lenormandia* et *Adamsiella* praesertim differt forma apicum, ordinatione areolarum, et ramificatione endogena.*

Member of Tribe Amansieae with unbranched or endogenously branched, broadly foliar blades erect from discoid to hapteral holdfast; fronds entire or lobed, margins smooth, crenate or dentate; midribs lacking; exogenous vegetative trichoblasts absent or reduced to one cell; adventitious vegetative trichoblasts sometimes present; pericentral cells five, 1-4 pseudopericentral cells usually present; apices emarginate or obcordate in outline, incurved in some species; medulla of two interdigitating layers of cells derived from dorsal and lateral pericentral cells; cortex single-layered; blade surfaces marked by irregularly ordered elliptic areolation; secondary cortication absent or present only in basal stipe or at bases of blades. Stichidia lanceoloid, irregularly disposed in aggregates directly on blade surfaces. Gametophytes dioecious, with procarps epibasal on reduced exogenous trichoblasts of arcuate dwarf adventitious branchlets irregularly aggregated on blade surfaces; cystocarps globose, sessile. Spermatangial capitula composed of a single sterile basal segment and 3-4 fertile segments without a sterile apical cell. Differing from *Lenormandia* and *Adamsiella* primarily in apical morphology, surface areolation and possession of endogenous branching.

Tetrasporophytes and gametophytes isomorphic, gametophytes dioecious. Thalli yellowish to rosy-pink to dark-red in colour, erect, arising from a discoid or hapteral holdfast and consisting of broad, flattened blades. Branching, where present, is endogenous and results in lobes or broad divisions of the mostly foliar blades. Growth of thalli apparently indeterminate throughout. Margins are entire, lobed, crenate or dentate. Blade surfaces with distinct, irregular elliptic areolation. Apices entire or emarginate to obcordate in outline, usually loosely incurved. Pericentral-cells five: two dorsal, two lateral and one ventral, the dorsal and lateral pericentral-cells each producing a series of wing-cells; in mature blades the two layers of cells may interdigitate giving the appearance in cross-section of a single medullary layer. The entire blade is corticated by a single layer of small cells. Secondary cortication is absent or present only on the stipe or base of the blades. Exogenous trichoblasts absent, reduced to a single cell, or found only on adventitious reproductive branchlets, otherwise replaced by adventitious vegetative trichoblasts. Tetrasporangia are produced in irregularly aggregated stichidia on blade surfaces, the stichidia cylindrical to lanceoloid, producing two tetrahedrally divided sporangia per fertile segment from the lateral (3rd and 4th) pericentral-cells. Cover cells two. Male and female reproductive structures arising from blade surfaces on dwarf adventitious branchlets which usually occur in irregular aggregations. Procarps consisting of a supporting cell, a four-celled carpogonial branch and both a lateral and a basal sterile-cell group.

Type species: *Aneurianna lorentzii* (Weber-van Bosse) L.E.Phillips, *comb. nov.*

Etymology: The genus name is derived from the original genus name *Aneuria* with the suffix *-anna* in recognition of the author of that genus Madame Anna Weber-van Bosse.

Distribution: Specimens of *Aneurianna* are known from South Africa (Natal), India, Japan, Philippines, Indonesia, East Timor and Australia (central Western Australia, Thursday Island and Great Barrier Reef, Queensland, Lord Howe Island, New South Wales and Norfolk Island) (Fig. 1), although many of the intervening localities are poorly collected and it is likely that the distribution is actually more extensive.

Remarks: Like several species of *Lenormandia* (eg. *L. spectabilis*, *L. latifolia*), this genus is distinguished from other members of the Amansieae by its foliar blades. *Aneurianna* differs from *Lenormandia* in its circular surface pattern of areolation (see Phillips, 2002, Fig. 1), presence of endogenous branching, and incurved or inflexed apex, in contrast to the rhombic areolation, absence of endogenous branching, and flat cleft apex of *Lenormandia*.

Key to the species of *Aneurianna*

1. Margins dentate; branching absent. *A. dentata*
1. Margins entire, lobed or crenate; endogenous branching usually present. **2**
2. Margins crenate; apex incurved and bearing dorsal row of exogenous trichoblasts or scars; distribution restricted to south-eastern coast of Africa. *A. nozawae*
2. Margins entire or lobed; apices flat or inflexed and without exogenous trichoblasts; distribution Indo-Pacific *A. lorentzii*

1. *Aneurianna lorentzii* (Weber-van Bosse) L.E.Phillips, *comb. nov.* **Figs 1-18**

Aneuria lorentzii Weber-van Bosse, 1911: 31; 1923: 371, pl. IX, figs 1-5; De Toni, 1924: 428; Okamura, 1929-1932: 4, pl. CCLIII; 1932:147; 1936: 889, fig. 415; Segawa, 1959: 120, pl. 71, fig. 583; Cribb, 1961: 54; May 1965:397; Nozawa, 1965: 76-80; Lewis, 1984: 61.

Lenormandiopsis lorentzii (Weber-van Bosse) Papenfuss, 1967:103; Wynne *et al.*, 1984: 274; Yoshida *et al.*, 1985: 267; 1990: 305; 1995: 149; Norris, 1987a: 82, figs 10, 11; Millar & Kraft, 1993: 55; Cribb, 1996: 103 + pl.; Silva *et al.*, 1996: 522; Kraft *et al.*, 1999: 24.

Aneuria parthasarathyi V.Krishnamurthy, 1967: 181, figs 1-20, pl. I

Lenormandiopsis parthasarathyi (V.Krishnamurthy) V.Krishnamurthy *et* H.Joshi, 1970: 25; Silva *et al.*, 1996: 523; Desikachary *et al.*, 1998: 329, pl. XXXI.

Lenormandiopsis sp. Allender & Kraft, 1983: 75.

Lectotype: Leiden L0276704 (Fig. 2). **Syntypes:** L0276705 and L0276706.

Type locality: **Lectotype** - Thursday Island, Torres Strait, Australia (*Lorentz*, 18 Jun 1907) **Syntypes** - east coast of Timor and Borneo Bank, Indonesia. The Thursday Island specimen is chosen as the Lectotype as it was collected by Lorentz in whose honour the species is named and is the specimen illustrated by Weber-van Bosse (1923, pl. IX, fig. 1) (Fig. 3).

Distribution: southern India; southern Japan; Philippines; Indonesia; East Timor; Queensland, Norfolk Island and Lord Howe Island, Australia (Fig. 1)

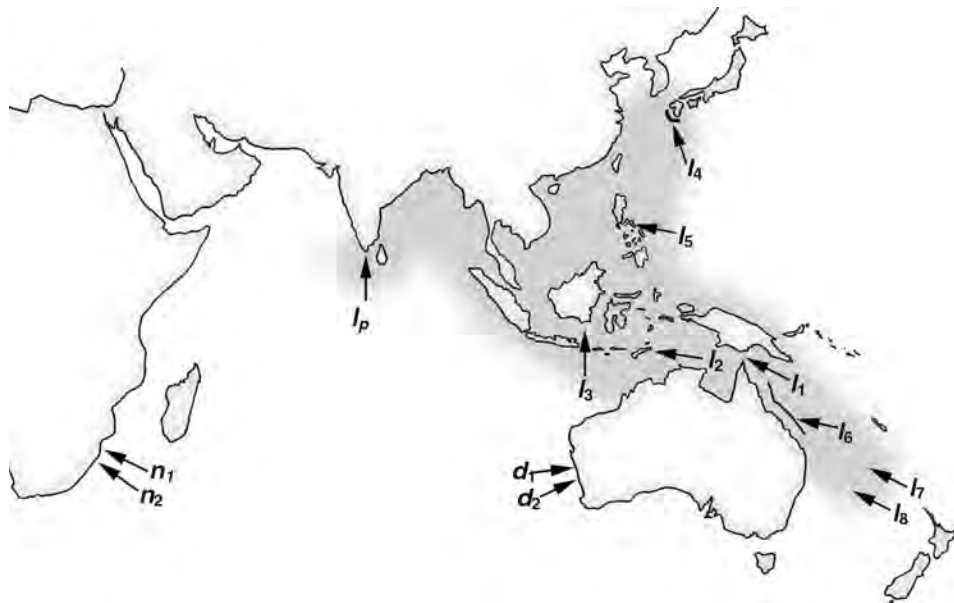
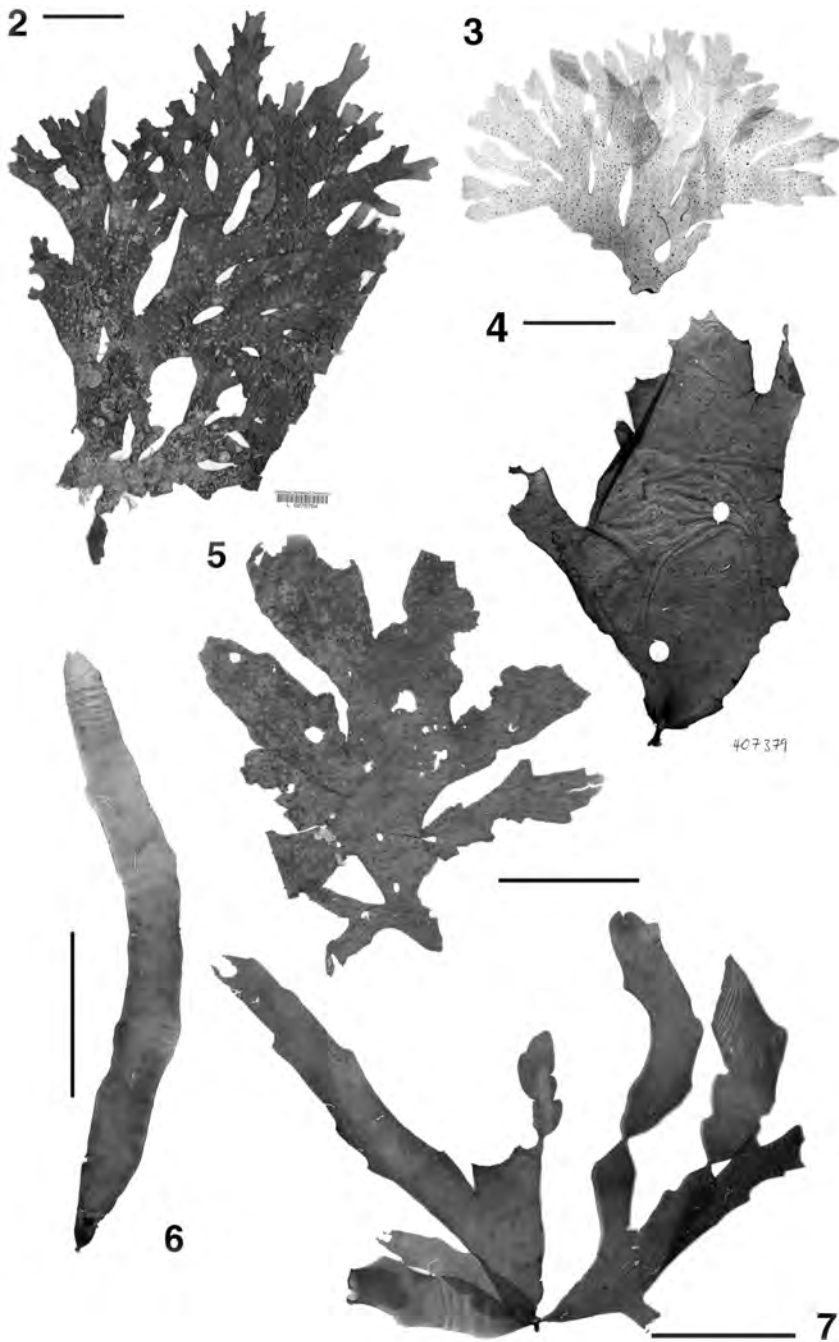


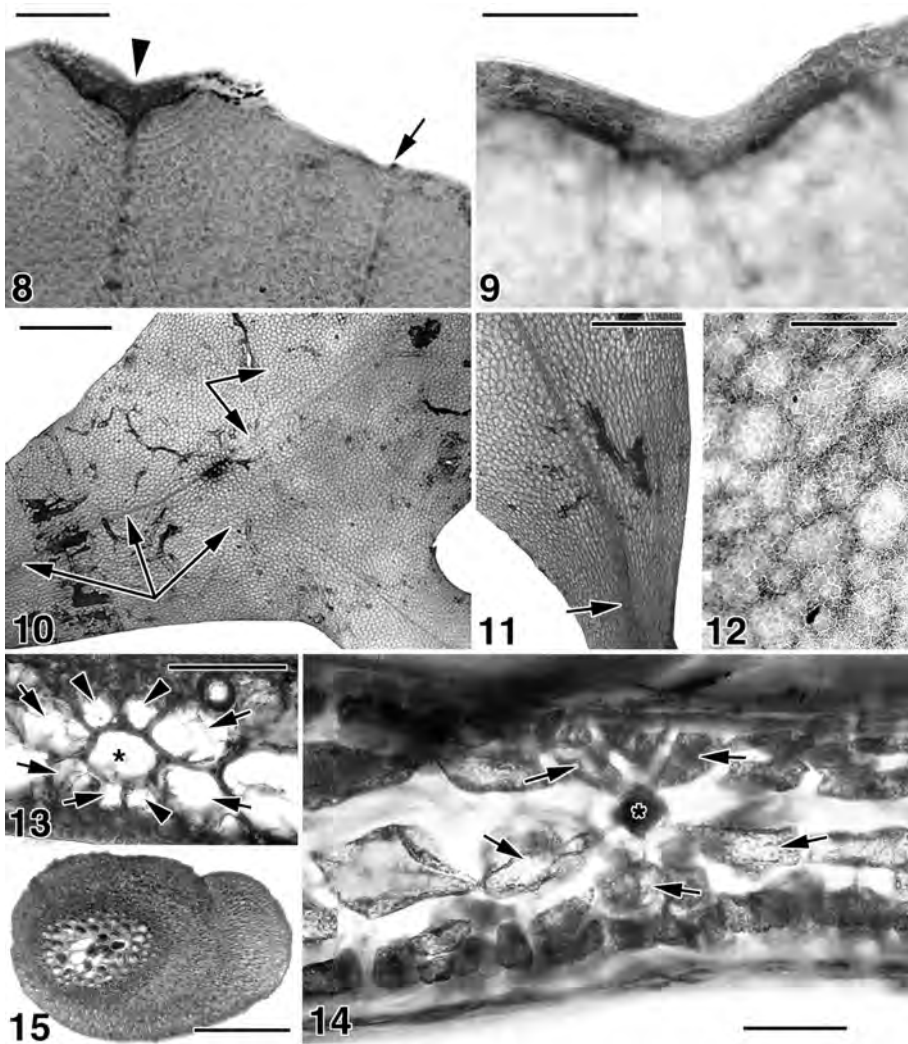
Fig. 1. Distribution and type localities of *Aneurianna* species. *A. lorentzii*. *I*₁ Thursday Island, Australia (lectotype locality); *I*₂ East Timor (syntype locality); *I*₃ Borneo Bank (syntype locality); *I*₄ southern Japan; *I*₅ Bulusan, Philippines; *I*₆ Great Barrier Reef, Queensland, Australia; *I*₇ Norfolk Island, New South Wales, Australia; *I*₈ Lord Howe Island, New South Wales, Australia; *I*_p Cape Comorin, India (type locality of *L. parthasarathyi*, which is reduced to synonymy with *A. lorentzii*). *A. nozawae*. *n*₁ Sodwana, Natal, South Africa (type locality); *n*₂ Cape Vidal, Northern Natal, South Africa; *A. dentata*. *d*₁ Port Denison, Western Australia (type locality); *d*₂ Jurien Bay, Western Australia.

Material Examined: **Japan**, Kumamoto Prefecture, Amakusa, Tomioka (*Yoshida*, 20 Aug 1956, SAP 049903, E). **India**, Idinthakarai, 30km N of Kanyakumari, drift (*Krishnamurthy*, 30 Jan 2002, LEP70-1,2,3, ⊕ E). **Philippines**, Luzon, Sorsogon Province, Bulusan, Dancalan, 1-10 metres depth (*Millar & Coppejans*, 21 Apr 1998, NSW 419126). **Indonesia**, Borneo, Borneo Bank, 40-50 metres (*Weber-van Bosse*, L0276706, SYNTYPE). **East Timor**, East coast, 2nd station, 41 metres (*Weber-van Bosse*, L0276705, SYNTYPE). **Australia, Queensland**, Thursday Island, (*Lorentz*, 18 Jun 1907 L0276704, LECTOTYPE); Ribbon Number Four Reef, 160 km north of Cairns, 32 metres depth (*Siotas*, 21 Nov 1985, MELU A041753/4); Russell Island, 30 metres depth (*Harada*, 28 Oct 1976, MELU 000008-000014/18); Black Reef, 60km north-east of Whitsunday Island, 4-6 metres depth (*Scott & McFadden*, 1 Dec 1978, MELU K15352, ⊕); Heron Island, Wistari Reef, 25 metres depth on coral rubble (*O'Brien & Siotas*, 23 Nov 1982, MELU A035947/8); channel, south end, 40 metres depth (*Larkum & Borowitzka*, 17 Sep 1974, MELU 000019/20); No place data (*Harada*, 5 Mar 1975, MELU 000015-17). **Australia, Norfolk Island**, Claytons Reef, north west of Nepean Island, 17 metres depth (*Millar & Richards*, 12 Dec 1994, NSW 397857/864); Little Organ, off Captain Cook memorial, 20 metres depth (*Marges*, 12 Jan 1997, NSW 407379). **Australia, Lord Howe Island**, "The Wall", 24-27 metres depth (*Kraft & Millar*, 16 Dec 1986, MELU K10841); Phillip Rock, 24 metres depth (*Kraft & Gabrielson*, 30 Jan 1982, MELU K10383).

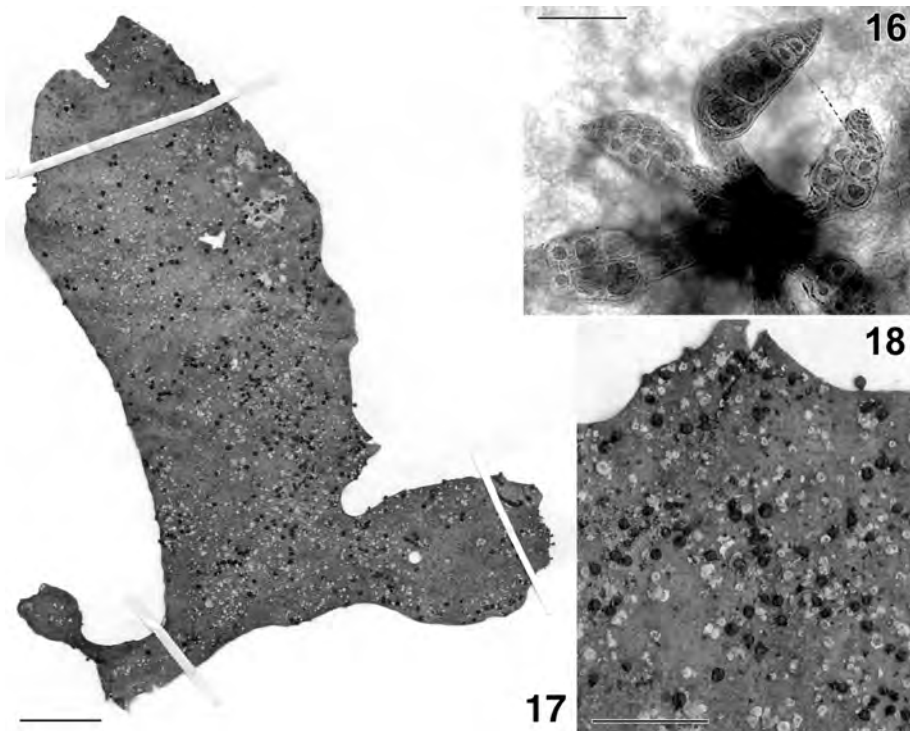
Habit and Anatomy: Plants arise from a small discoid holdfast and may reach 30 cm in length (Figs 2-6). There may be a short terete, occasionally branched, stipe at the base of the plant (Fig. 7), but more usually the blade is single, broadening rapidly



Figs 2-7. *Aneurianna lorentzii* (Weber-van Bosse) L.E. Phillips *gen. et comb. nov.* (2 = Leiden L0276704, 4 = NSW 407379, 5 = LEP 70-1, 6 = MELU 000018, 7 = MELU 000008). 2. Lectotype specimen from Thursday Island. Scale = 5 cm. 3. Weber-van Bosse's illustration (1923, Pl. IX, fig. 1). 4-7. Specimens illustrating the range of variation in overall habit. Scales = 5 cm.



Figs 8-15. *Aneurianna lorentzii* (Weber-van Bosse) L.E. Phillips *gen. et comb. nov.* (8, 10-12 = MELU 000008, 9 = L 0267604, 13-15 = MELU K10383). **8-9.** Apical portions of blades. (8) shows an inclinate main apex (arrowhead) and unfolded secondary apex (arrow). Scales = 200 μ m. **10.** Detail of blade showing primary and secondary midribs (arrows). Note also circular surface areolation. Scale = 5 mm. **11.** Close-up near transition of stalk to blade detailing percurrent central axis. Scale = 2 mm. **12.** Detail of surface cell pattern with irregular elliptical areolation visible through a layer of small cortical cells. Scale = 500 μ m. **13-14.** Cross-sections through middle of older (13) and younger (14) blades showing central-axial cell (asterisk) and five pericentral cells (arrows). Pseudopericentral cells may also be present (arrowheads, 13). Scales 13 = 200 μ m, 14 = 50 μ m. **15.** Cross-section through stipe showing secondary cortication with growth rings. Scale = 1 mm.



Figs 16-18. *Aneurianna lorentzii* (Weber-van Bosse) L.E. Phillips *gen. et comb. nov.* (16 = MELU A035947, 17-18 = SAP 49903) **16.** Lanceolate tetrasporangial stichidia with terete bases arise in irregular aggregations directly from the blade surface. Scale = 200 μ m. **17.** Habit of female specimen. Scale = 2 cm. **18.** Detail of female gametophyte with mature cystocarps scattered on the blade surface. Scale = 1 cm.

from the holdfast to an irregularly shaped, flattened blade (Figs 2, 4, 5). There is a great variety in the size and shape of the blades, some specimens having many lobes or branches (Figs 2, 5, 7 and Weber-van Bosse, 1923: pl. IX, fig1), others being narrow, simple and linear (Fig. 6). Apices are often grazed or worn away but, where present, are inconspicuous and sometimes inflexed (Figs 8, 9). Exogenous trichoblasts are absent from the apices (Fig. 9). Faint midribs are usually distinguishable (Figs 10, 11), as are the interior axes of the endogenous branchings of the central-axial filaments (Fig. 10) and the axial-filaments of the laterals leading to subsidiary apical cells at the margins (Fig. 8). The surface of the blade is covered with a single layer of small irregularly-shaped cortical cells, through which the irregular circular areolation of the blade is visible (Figs 10, 12). In cross-section the blades are composed of a central-axial cell, five pericentral cells (two dorsal, two lateral and one ventral) (Fig. 14) and in older blades two to four pseudopericentral cells may be present (Fig. 13). The cortex is composed of a single layer, one to two cells thick, of small isodiametric cells (Figs 13, 14). Slight secondary cortication may be present at the base of older blades (Fig. 15).

Tetrasporangial stichidia arise in aggregations on the surface of the blades, are lanceoloid with a terete base, and bear two tetrasporangia per fertile segment (Fig. 16). Young female gametophytes were not available for exami-

nation, but Nozawa (1965) has described the procarps as arising in a dorsal series on adventitious polysiphonous branchlets which are incurved and found in aggregations on the surface of the blade. The procarp is typically amansoid in composition, one of the pericentral cells acting as the supporting cell and producing a four-celled carpogonial branch and both a lateral and basal sterile group. Mature cystocarps are 1- 1.7 mm in diameter and are irregularly scattered on the surface of the blade (Figs 17, 18).

Male gametophytes were not available for examination but spermatangial branches have been reported by Krishnamurthy (1967, for *Aneuria parthasarathyi*) as arising in two alternating dorsal series on adventitious polysiphonous branchlets which are incurved and found in clusters irregularly spaced on the surface of the blade. The spermatangial axis is a modified reduced trichoblast in which the basal cell remains sterile and the upper cells form spermatangial parent-cells.

Remarks: This species is variable in habit and has a widespread Indo-Pacific distribution. It has, however, been fairly infrequently recorded, although some collections (eg. MELU 000008-000014/18) consist of numerous specimens. *Lenormandiopsis parthasarathyi* is here reduced to synonymy with *Aneurianna lorentzii*. The description of *Aneuria parthasarathyi* (Krishnamurthy, 1967) distinguishes it from *Aneurianna lorentzii* "in being smaller and mostly unbranched". Despite repeated attempts, I have been unable to locate the type specimens of *Aneuria parthasarathyi*, but have examined material collected by Professor Krishnamurthy from a nearby Indian location (see **Material Examined** above, Fig. 5). As has been shown, *Aneurianna lorentzii* is highly variable in general outline and size, sometimes even within single collections, and the Indian material falls within the range of size and degree of branching exhibited by other specimens of *A. lorentzii*.

2. *Aneurianna nozawae* (R.E. Norris) L.E. Phillips, comb. nov. Figs 1, 19-30

Lenormandiopsis nozawae R.E. Norris, 1987a: 87, fig.1-9; 1987b: 213, figs 1-14; Silva *et al.*, 1996: 523.

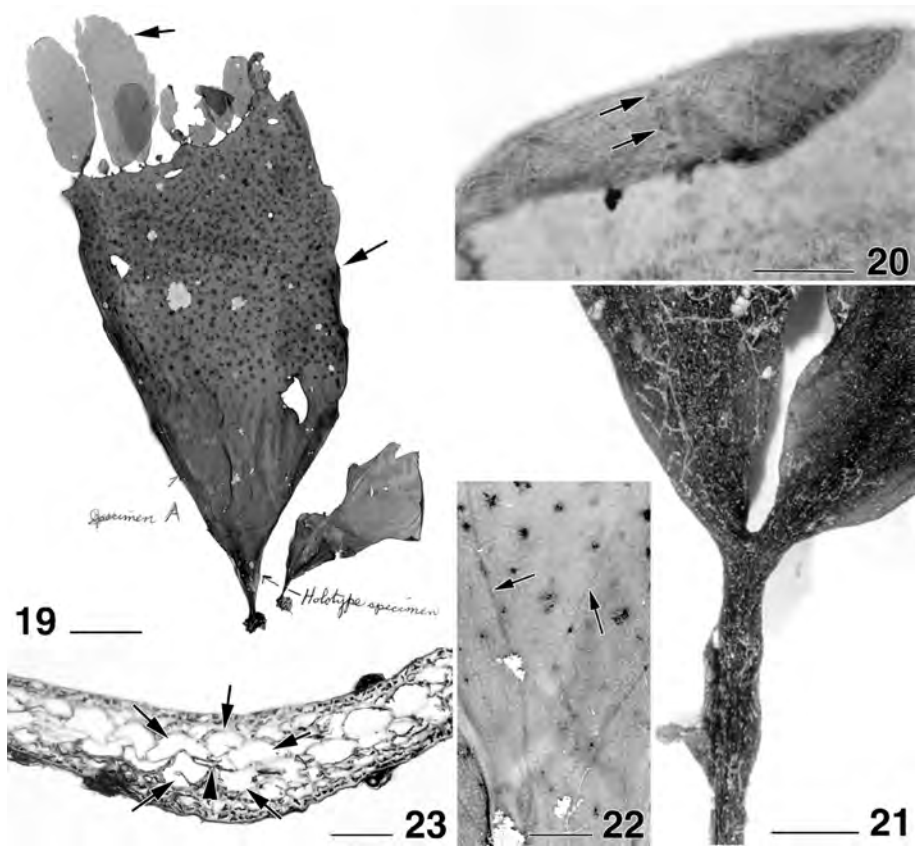
Holotype: NU 9135 (specimen A) (Fig. 19)

Type Locality: off Jesser Point, Sodwana, Ubombo District, Natal, South Africa (Fig. 1)

Distribution: Natal, South Africa

Selected Specimens: South Africa, Natal, Ubombo District, Sodwana, off Jesser Point, coral and sand substrate, 46-47 metres depth (*Dench*, 6 May 1985, NU 9135 HOLOTYPE and ISOTYPES, NU 9134 ISOTYPE ⊕); Ubombo District, 2.5km east of Sodwana Bay, on stable sand, 56 metres depth (*Dench & Smith*, 16 May 1986, NU 9722/3 ⊕, NU9725 Γ E); Northern Natal, Cape Vidal, drift (*Meyer*, 14 Jun 1980, NU 3101).

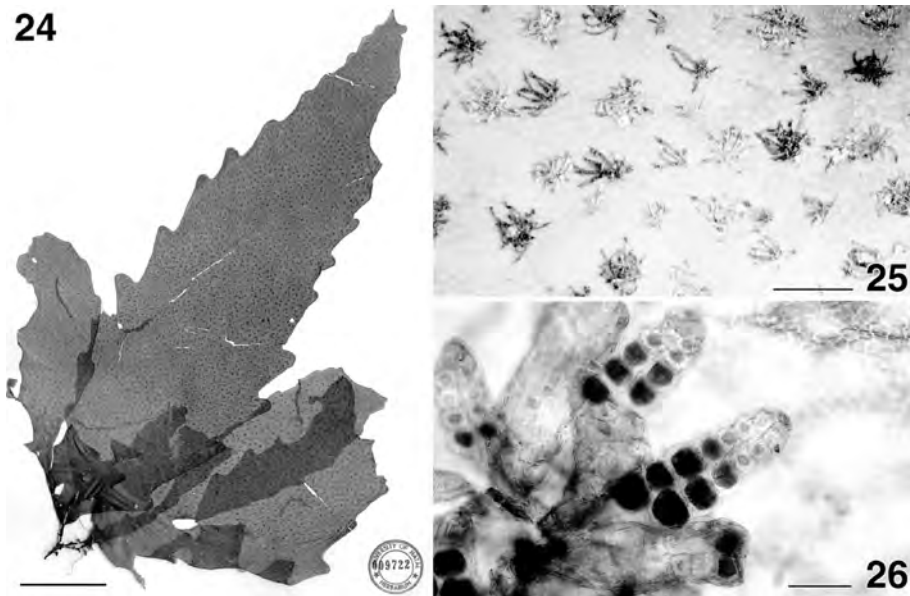
Habit and Anatomy: Plants may reach 40 cm in length (Fig. 24) and are found at depths of approximately 45-60 metres. Colour in fresh plants is bright to dark pink, although drift specimens may be brown or yellowish. Thalli arise from a discoid holdfast (Fig. 19) that may give rise to a short, terete, sometimes branched (Figs 21, 24) stipe or that widens rapidly to a flattened blade (Fig. 19). Blades vary in size and shape but, where undamaged, margins are usually broadly crenate (Fig. 19, 24). Apices are often grazed or worn away but, where present, are incurved and bear a series of dorsal exogenous trichoblasts that are only one to three cells in length and are rapidly deciduous, leaving conspicuous scars (Fig. 20). Mid-ribs are usually indistinguishable; the surface of the blade is marked with irregular circular areolation (Fig. 22). Branching is endogenous (Fig. 22); the marginal crenations corresponding to the apices of lateral branches. Slight secondary cortication may be present at the base of older blades and on the short basal stalks (Fig. 21).



Figs 19-23. *Aneurianna nozawae* (R.E. Norris) L.E. Phillips *comb. nov.* (19, 20, 22 = NU 9135; 21, 23 = NU 9722). **19.** Holotype specimen (tetrasporophyte) that shows extensive regeneration of blades from the damaged apical portion of the primary blade. Both the primary and secondary blades show the coarsely sinuous/crenate profile (arrows) characteristic of the species. Scale = 2 cm. **20.** Inrolled apical portion with dorsal row of exogenous trichoblast scars (arrows). Scale = 200 μ m. **21.** Basal portion of thallus with slightly winged stipe and two blades arising from it. Scale = 2 mm. **22.** Surface view of blade showing the irregular elliptic surface areolation and midlines of endogenous lateral branches (arrows). Scale = 5 mm. **23.** Cross-section of blade showing central-axial cell (arrowhead) and five pericentral cells (arrows). This cross-section is slightly "V"-shaped in profile. Scale = 200 μ m.

Tetrasporangial stichidia arise in aggregations on the surface of the blades (Figs 24, 25), are lanceoloid with a terete base, and bear two tetrasporangia per fertile segment (Fig. 26). Plants are dioecious, female gametophytes (Fig. 27) producing procarps in a dorsal series on adventitious polysiphonous branchlets, which are incurved and found in aggregations on the surface of the blade. The procarp is typically amansoid in composition, and mature cystocarps are 1-1.7 mm in diameter (Figs 27, 28).

Male gametophytes (Fig. 30) produce spermatangial branches in dorsal series on adventitious polysiphonous branchlets, which are incurved and found in clusters irregularly spaced on the surface of the blade (Figs 29, 30). The



Figs 24-26. *Aneurianna nozawae* (R.E. Norris) L.E. Phillips *comb. nov.* (NU 9722). **24.** Habit of tetrasporophyte. Scale = 5 cm. **25.** Aggregates of tetrasporangial stichidia arranged irregularly on surface of fronds. Scale = 2 mm. **26.** Tetrasporangial stichidia bearing two sporangia per fertile segment. Scale = 200 μ m.

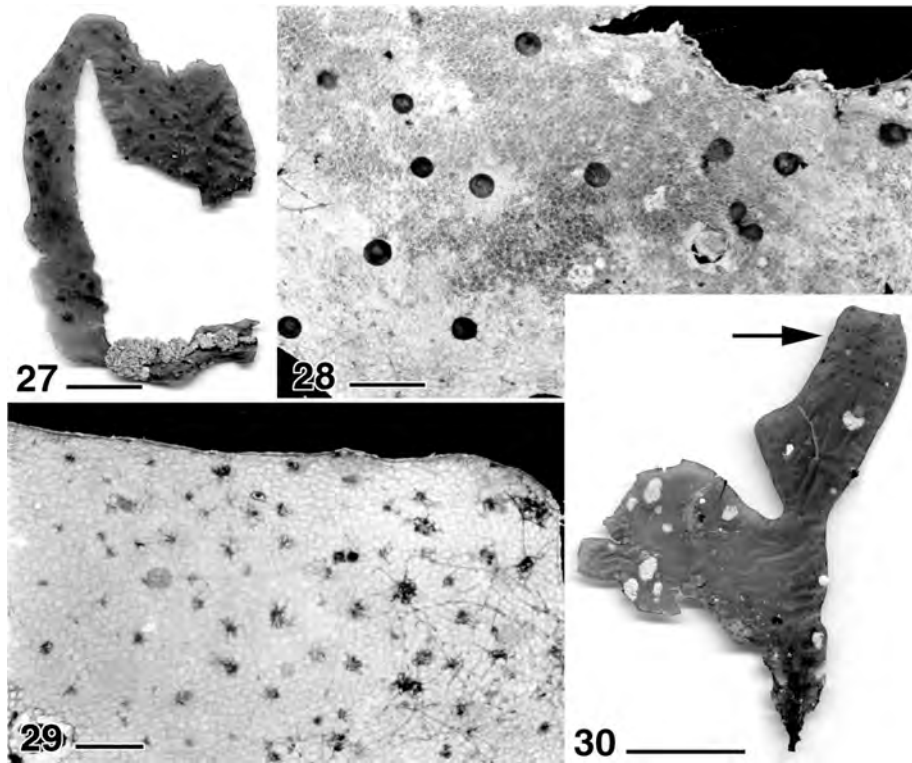
spermatangial axis is a modified reduced trichoblast in which the basal cell remains sterile, and the upper cells form spermatangial parent-cells.

Remarks: When describing this species, Norris (1987a) had only a single putative specimen of *L. lorentzii* for comparison. He considered the features that distinguished the two species to be the difference in colour and the length of the tetrasporangial stichidia. In this study I have examined not only all the material Norris studied, but also many specimens of *L. lorentzii* including the type specimens. In my opinion, Norris's specimen of "*A. lorentzii*" from Cape Vidal (NU 003101) belongs to the same species as all the other South African specimens. The difference in colour is attributable to its collection from drift, and the difference in size of the stichidia merely part of the natural variation commonly seen in this character within a species. Nevertheless, I believe the South African specimens belong to a separate species from Asian and Australian collections, and consider the distinguishing characters to be the presence of apical trichoblasts and their scars and the broadly crenate margins. In damaged and grazed specimens that have lost apices and margins, it would be difficult to distinguish between the two species, but as no *bona fide* specimens of *A. lorentzii* are known to have been collected from South Africa, the disjunct distribution may be considered a further species character.

3. *Aneurianna dentata* L.E. Phillips, *sp. nov.*

Figs 1, 31-40

Aneurianna laminae simplicibus ellipticis ad 30 cm longis et 8 cm latis, apicibus laxe incurvatis, marginibus dentibus triangularibus simplicibus vel compositis ad 4 mm longis ornatis; trichoblastis vegetativis adventitiis dispersis in superficiebus



Figs 27-30. *Aneurianna nozawae* (R.E. Norris) L.E. Phillips *comb. nov.* (NU 9725). **27.** Habit of female gametophyte. Scale = 1 cm. **28.** Surface of female gametophyte showing scattered cystocarps. Scale = 2 mm. **29.** Surface view of fertile region of male gametophyte with scattered groups of fertile trichoblasts. Scale = 2 mm. **30.** Habit of male gametophyte. Fertile region is to the top right (arrow). Scale = 2 cm.

laminarum, 150-200 μm longis, ramosissimis; *stichidiis lanceoloideis*, *basibus sterilibus angustis teretibus*. *Plantae gametangiales ignotae*.

The *Aneurianna* with simple, elliptic blades to 30 cm in length by 8 cm in width; apices loosely incurved; blade margins with regularly spaced, simple or compound triangular dentations to 4 mm in length. Adventitious vegetative trichoblasts irregularly scattered on blade surfaces, 150-200 μm in length, highly branched. *Stichidia* lanceoloid, with narrow terete sterile bases. Gametangial plants unknown.

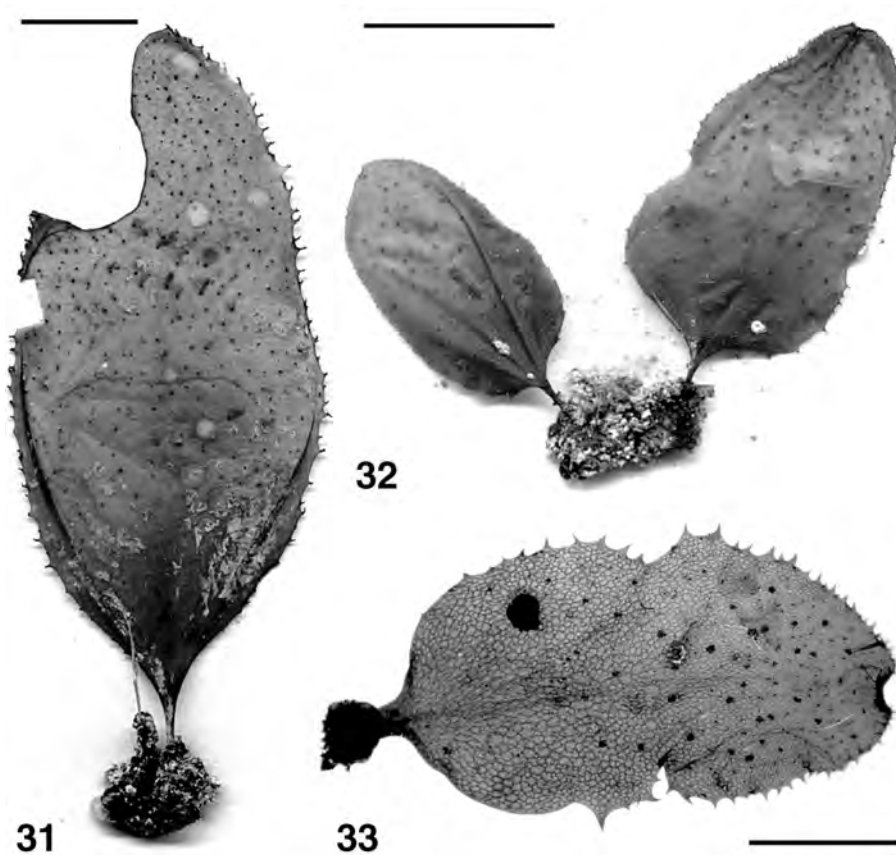
Holotype: MELU K7043 (Fig. 31)

Type Locality: Port Denison, Western Australia (Fig. 1)

Etymology: named for its distinctive marginal dentations

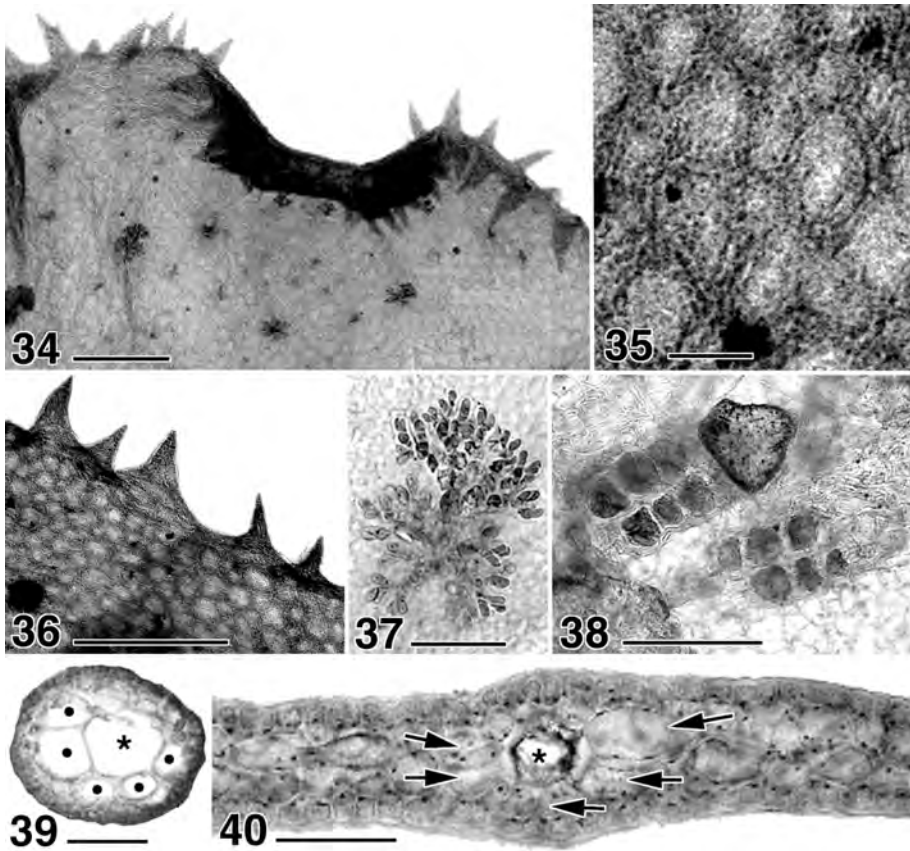
Distribution: known only from mid-west coast of Western Australia (Fig. 1).

Selected Specimens: **Australia, Western Australia**, Port Denison, at 10-12 m depths (*Kraft & Allender*, 10 Aug 1979, MELU K7043, HOLOTYPE and ISOTYPES); drift (*Kraft*, 6-7 Jul 1966, MELU K1785, \oplus) (*Kerry*, 6 Sep 1975, MELU K5748); Jurien Bay, 2 m depths on rock in sand (*Huisman*, 26/27 Oct 2000, MURU JB673/4/7, JB680, JB691/2/4/5/7/8).



Figs 31-33. *Aneurianna dentata* L.E. Phillips *sp. nov.* (MELU K7043). **31.** Holotype from Port Denison, Western Australia. Scale = 1 cm. **32, 33.** Isotypes with short stipes, flattened elliptic to ovate blades with distinct marginal dentations and elliptical areolation patterns on blade surfaces. Scales 32 = 10 mm, 33 = 5 mm.

Habit and Anatomy: Plants arise from a discoid to hapteral holdfast and have a short, terete stipe that flattens to a simple, elliptic to ovate blade up to 30 cm in length by 8 cm in width (Figs 31-33). The apex is loosely incurved (Figs 32, 34), and the margins bear fairly regular tooth-like projections (Figs 31-34, 36). Both the apex and marginal dentations may be worn away in older specimens. The dentations are determinate, roughly triangular (Fig. 36), up to 4 mm long and 3 mm wide at the base, and may themselves be dentate. In surface view the blades bear the irregular circular areolation characteristic of the genus (Fig. 35), but show no sign of a midrib (Figs 31-33). Adventitious vegetative trichoblasts may arise irregularly over the surface of the blade (Figs 32, 34, 37) and are small at first (150 to 200 μm) (Fig. 37) but become elongate and highly branched. In cross-section the blade and the marginal spines (Fig. 39) are composed of a central-axial cell and five pericentral cells (two dorsal, two lateral and one ventral) (Fig. 40). The dorsal and lateral pericentral cells of the blade each produce a row of wing cells that interlock so that the medulla appears to be composed of a single layer



Figs 34-40. *Aneurianna dentata* L.E. Phillips *sp. nov.* (34-37 = MELU K7043, 38-39 = MURU JB 673, 40 = MELU K1785). **34.** Apical portion of blade with loosely incurved apex and marginal dentations. Scale = 500 μm . **35.** Detail of surface cell pattern with irregular elliptical areolation. Scale = 500 μm . **36.** Detail of marginal dentations. Scale = 1 mm. **37.** Dwarf adventitious vegetative trichoblasts arising directly from the blade surface. Scale = 100 μm . **38.** Tetrasporangial stichidia with paired sporangia in each fertile segment. Scale = 250 μm . **39.** Cross-section of marginal spine showing irregular arrangement of central-axial cell (asterisk) and five pericentral cells (dots). Scale = 200 μm . **40.** Cross-section of middle of blade with central-axial cell (asterisk), five pericentral cells (arrows) and several dorsal and ventral pseudopericentral cells. Scale = 100 μm .

of thin-walled vacuolate cells. The cortex is composed of a single layer, one to two cells thick, of small isodiametric cells. The cross-sections may describe a shallow "V" shape in outline. Secondary cortication is absent except in the stipe.

Stichidia arise in aggregations that are irregularly scattered on both surfaces of the blade. They have a narrow terete section at their base, widening to a thicker, cylindrical fertile section that bears tetrasporangia in parallel longitudinal rows, two per fertile segment (Fig. 38). Male and female gametophyte plants have not been collected.

Remarks: This species is distinct from other species of *Aneurianna* by its marginal dentations, although these may be eroded away in older/larger specimens. It also differs from most specimens of *A. lorentzii* in the lack of branching. Plants that

most closely resemble *A. dentata* in overall habit are those of *Lenormandia latifolia*, from which it differs in the incurved apex, marginal dentations, and circular surface areolation in contrast to the flat, cleft apex, smooth margins and rhombic areolation of *L. latifolia*.

MOLECULAR RESULTS

The results of the maximum likelihood analysis are shown in Fig. 41. The distance (neighbor-joining) analysis resulted in a tree with similar topology, except that the *Adamsiella* clade and the *Epiglossum* clade formed a sibling clade (60% bootstrap support) to the one containing the *Lenormandia* species. Parsimony analysis resulted in six most-parsimonious trees (Length = 222 steps, CI = 0.856, RI = 0.712, RC = 0.609, HI = 0.144) which differed from each other in the placement of *Neurymenia* (either sibling to *Aneurianna* or sibling to the

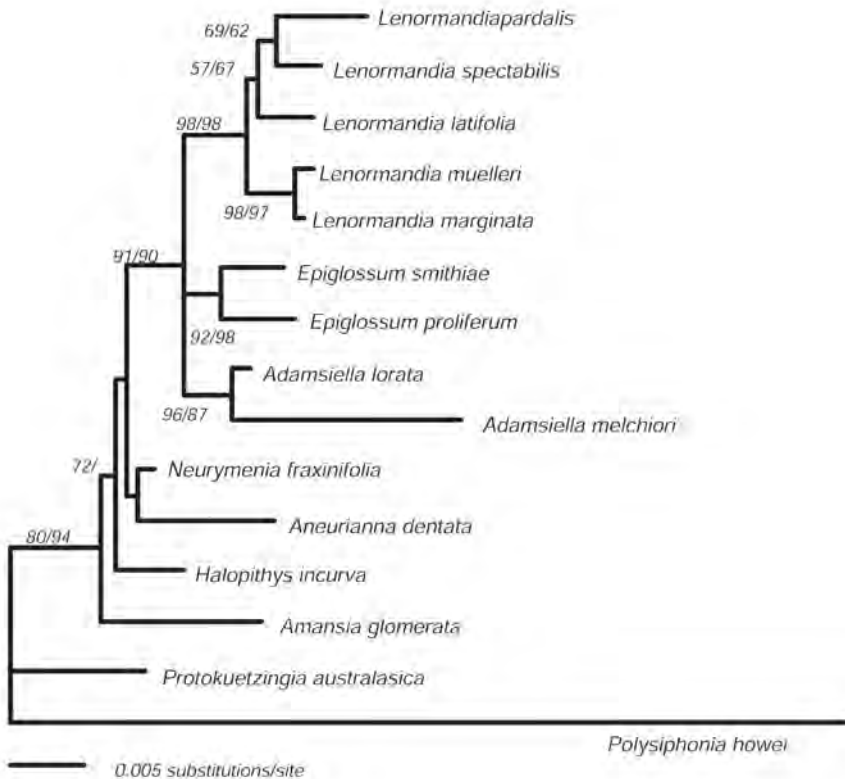


Fig. 41. Maximum Likelihood Phylogram. Numbers at internal nodes represent bootstrap support (1000 replicates) for neighbor-joining (left) and parsimony (right) analyses.

“*Lenormandia* complex” clade, i.e. the clade containing *Lenormandia*, *Adamsiella* and *Epiglossum*) and in the relationships within the *Lenormandia* complex. When not sibling to *Neurymenia*, *Aneurianna* was sibling to the large clade containing the “*Lenormandia* complex” and *Neurymenia*. In all analyses the composition of the *Lenormandia* complex remained stable and was well supported (91% distance, 90% parsimony). There was no evidence for any close relationship between *Aneurianna dentata* and *Lenormandia* (previously *Lenormandiopsis*) *latifolia*. Although in some analyses *Aneurianna* formed a clade with *Neurymenia fraxinifolia*, this relationship was not well supported.

DISCUSSION AND CONCLUSIONS

In a previous paper (Phillips, 2002) it was shown that the type species of *Lenormandiopsis*, *L. latifolia*, conformed in both anatomical characters and 18S rDNA sequences to *Lenormandia*. It was, as a consequence, returned to that genus in which it had originally been placed. This investigation of the remaining species of *Lenormandiopsis* has highlighted their differences from *Lenormandia latifolia* and, indeed, the other members of the *Lenormandia* complex of genera (*Lenormandia*, *Adamsiella*, *Epiglossum*). The major character that separates *Lenormandia* and *Aneurianna* is the presence/absence of endogenous branching. Endogenous branching is seen in all members of the Amansieae with the exception of the genera *Lenormandia*, *Adamsiella* and *Epiglossum*. The separation of the species removed to *Aneurianna* from *Lenormandia latifolia* is also supported by the molecular analyses.

Aneurianna differs from other members of the Amansieae in the broadly foliar blades resulting from apparently indeterminate growth of the wings of the blades. The development of lateral branches as extensions of the margins of the blades also enhances the broad and irregular outline of the thalli. The presence of incurved apices is similar to that of the majority of the Amansieae, as is the development of a dorsal row of exogenous trichoblasts seen in *A. nozawae*.

In some of the molecular analyses *Aneurianna dentata* grouped with *Neurymenia fraxinifolia*, although this relationship was not well supported. *Neurymenia*, like *Aneurianna*, has broad foliar blades but differs in that the blades are regular in outline. The most distinctive character of *Neurymenia* is the presence of lateral veins on the blades, one that sets *Neurymenia* apart from all other members of the Amansieae.

Although the several species of *Aneurianna* have been collected only infrequently, on some occasions substantial numbers of thalli have been found (eg. *A. lorentzii*, Russell Island, Queensland, Oct 1976, MELU 000008-14/16, *A. dentata*, Jurien Bay, WA, Oct 2000, MURU JB673/4/7, JB680, JB691/2/4/5/7/8). This suggests that populations may be more extensive than the frequency of its collection indicates. In addition, these species often grow deep and in remote or poorly collected areas, and it is expected that the distributions of all species are more widespread than presently known.

Acknowledgements. I am grateful to Dr G. T. Kraft for the use of the facilities in his laboratory where this work was largely conducted. I am indebted to John Huisman and Professor V. Krishnamurthy for vital collections of *Aneurianna dentata* and *Lenormandiopsis parthsarathyi* respectively. I am grateful also to the curators of the

herbaria at Murdoch University, Murdoch, Western Australia (MURU), Royal Botanic Gardens of New South Wales, Sydney (NSW), University of Natal, KwaZulu-Natal Province, South Africa (NU) and The Graduate School of Science, Hokkaido University, Sapporo, Japan (SAP) for loans of their material. The Latin diagnoses were provided by Mark Garland. The author was financially supported by a Commonwealth of Australia, Australian Postgraduate Award.

REFERENCES

- AGARDH J.G., 1892 — *Analecta Algologica. Acta Universitatis lundensis* 28: 1-182.
- ALLENDER B.M. & KRAFT G.T., 1983 — The marine algae of Lord Howe Island (New South Wales): the Dictyotales and Cutleriales (Phaeophyta). *Brunonia* 6: 73-130.
- CRIBB A.B., 1961 — Some marine algae from Thursday Island. *Papers of the University of Queensland botany department* 4: 51-59.
- CRIBB A.B., 1996 — *Seaweeds of Queensland, a naturalist's guide*. Brisbane, The Queensland Naturalists' Club Inc, 130 p.
- DESIKACHARY T.V., KRISHNAMURTHY V. & BALAKRISHNAN M.S., 1998 — *Rhodophyta. Vol. II – Part IIB*. Chennai, Madras Science Foundation, 359 p., 89 figs, xxxi pls.
- DE TONI G.B., 1924 — *Sylloge algarum omnium hucusque cognitarum. Vol. 6. Florideae. Sectio 5. Additamenta*. Padua, Privately published, xi + 767 p.
- DUMORTIER B.C., 1822 — *Commentationes botanicae*. Tournay. 116 p.
- GILBERT D.G., 1995 — *SeqPup, a biological sequence editor and analysis program for Macintosh computers*. Available via anonymous ftp to ftp.bio.indiana.edu.
- HASEGAWA M., KISHINO H. & YANO K., 1985 — Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of molecular evolution* 22: 160-174.
- KRAFT G.T., LIAO L.M., MILLAR A.J.K., COPPEJANS E.G.G., HOMMERSAND M.H. & FRESHWATER D.W., 1999 — Marine benthic red algae (Rhodophyta) from Bulusan, Sorsogon Province, southern Luzon, Philippines. *The Philippine scientist* 36: 1-50.
- KRISHNAMURTHY V., 1967 — *Aneuria parthasarathii* sp. nov., a dorsiventral Rhodomelaceae from Cape Comorin, South India. *Phykos* 5: 181-186.
- KRISHNAMURTHY V. & JOSHI H.V., 1970 — *A check-list of Indian marine algae*. Bhavnagar, Central Salt and Marine Chemicals Research Institute, 36 p.
- KYLIN H., 1956 — *Die Gattungen der Rhodophyceen*. Lund, CWK Gleerups Förlag, xv + 673 p., 458 figs.
- LEWIS J.A., 1984 — *Checklist and bibliography of benthic marine macroalgae recorded from northern Australia. I. Rhodophyta*. Melbourne, Department of Defence Material Research Laboratory, 97 p.
- MAY V., 1965 — A census and key to the species of Rhodophyceae (red algae) recorded from Australia. *Contributions from the NSW National Herbarium* 3: 349-429.
- MILLAR A.J.K. & KRAFT G.T., 1993 — Catalogue of marine and freshwater red algae (Rhodophyta) of New South Wales, including Lord Howe Island, south-western Pacific. *Australian systematic botany*. 6: 1-90.
- NORRIS R.E., 1987a — *Lenormandiopsis* (Rhodomelaceae), newly recorded from Africa, with a description of *L. nozawae* sp. nov. and comparison with other species. *Japanese journal of phycology* 35: 81-90.
- NORRIS R.E., 1987b — Structure and reproduction in *Lenormandiopsis nozawae* (Rhodomelaceae, Rhodophyta). *Cryptogamie, Algologie* 8: 211-221.
- NOZAWA Y., 1965 — On the female organ of “Sujinashigusa”, *Aneuria lorenzii* Weber van Bosse from Japan. *Bulletin of the Japanese society for phycology* 8: 76-80.
- OKAMURA K., 1929-1932 — *Icones of Japanese algae. Vol. 6*. Tokyo. pp. 101 + 96, pls. CCLI-CCC.

- OKAMURA K., 1932 — The distribution of marine algae in Pacific waters. *Records of oceanographic works in Japan* 4: 30-150.
- OKAMURA K., 1936 — *Nihon Kaisoshi (Japanese algae)*. Tokyo, Uchida Rokakuho Publishing Co. Ltd, 11 + 964 + 11 p. (in Japanese)
- PAPENFUSS G.F., 1967 — Notes on algal nomenclature - V. Various Chlorophyceae and Rhodophyceae. *Phykos* 5: 95-105.
- PHILLIPS, L. E., 2000 — Taxonomy of the New Zealand-endemic genus *Pleurostichidium* (Rhodomelaceae, Rhodophyta). *Journal of phycology* 36: 773-786.
- PHILLIPS L.E., SAUNDERS G.W., CHOI H.-G. & KRAFT G.T., 2000 — The morphology, taxonomy and molecular phylogeny of *Heterocladia* and *Trigenea* (Rhodomelaceae: Rhodophyta), with delineation of the little known tribe Heterocladieae. *Journal of phycology* 36: 199-219.
- PHILLIPS L.E., 2001 — Morphology and molecular analysis of the Australasian monotypic genera *Lembergia* and *Sonderella* (Rhodomelaceae, Rhodophyta), with a description of the tribe Sonderelleae trib. nov. *Phycologia* 40: 487-499.
- PHILLIPS L.E., 2002 — Taxonomy and molecular phylogeny of the red algal genus *Lenormandia* (Rhodomelaceae, Ceramiales). *Journal of phycology* 38: 184-208.
- SEGAWA S., 1959 — *Coloured illustrations of the seaweeds of Japan*. Osaka, Hoikusha, xviii + 175 p. + 72 pls.
- SILVA P.C., BASSON P.W. & MOE R.L., 1996 — *Catalogue of the benthic marine algae of the Indian Ocean*. Los Angeles, University of California Press, 1259 p.
- SWOFFORD D.L., 1999 — *PAUP - Phylogenetic Analysis Using Parsimony, Version 4.0.0b2*. Washington D.C., Smithsonian Institution.
- WEBER-VAN BOSSE A., 1911 — Notice sur quelques genres nouveaux d'algues de l'Archipel Malaisien. *Annales du jardin botanique de Buitenzorg* 24: 25-33.
- WEBER-VAN BOSSE A., 1923 — Liste des algues du Siboga. III. Rhodophyceae. Seconde partie. Ceramiales. *Siboga-Expeditiem Monograph* 59c: 311-392.
- WYNNE M.J., MILLAR A.J.K. & KRAFT G.T., 1984 — *Platysiphonia marginalis* sp. nov. (Delesseriaceae), a new red alga from eastern Australia. *Phycologia* 23: 273-279.
- YOSHIDA T., NAKAJIMA Y. & NAKATA Y., 1985 — Preliminary check-list of marine benthic algae of Japan - II. Rhodophyceae. *Japanese journal of phycology* 33: 249-275.
- YOSHIDA T., NAKAJIMA Y. & NAKATA Y., 1990 — Check-list of marine benthic algae of Japan (revised in 1990). *Japanese journal of phycology (Sôru)* 38: 269-320.
- YOSHIDA T., YOSHINAGA K. & NAKAJIMA Y., 1995 — Check list of marine algae of Japan (revised in 1995). *Japanese journal of phycology (Sôru)* 43: 115-171.