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Neoholmesia natalensis, a new member of the Delesseriaceae (Rhodophyceae) from South Africa

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Neoholmesia natalensis sp. nov. is described from the Natal coast of South Africa on the basis of two collections (Park Rynie and Palm Beach). Tetrasporic specimens but no sexual specimens were observed. The apical organization of the blades conforms to that of the Membranoptera Group. The blades become polystromatic. The central midlines of the blades persist as thickened, cartilaginous axes, from which new crops of blades arise. Tetrasporangia are produced on blades arising from these thickened axes; these fertile blades are indistinguishable from vegetative blades arising in a similar manner. The well developed basal system of perennial axes and the restriction of tetrasporangia to a single layer on the adaxial surface of the blades are distinctive features of this species. *Neoholmesia neurymenioides* (OKAM.) WYNNE comb. nov. is also proposed.

Key Index Words: *Delesseriaceae*; Heteroglossum; *marine algae*; *Membranoptera Group*; Neoholmesia natalensis; Neoholmesia neurymenioides; *Rhodophyceae*; *South Africa*.

A catalogue of the benthic marine algae of South Africa, containing a total of 547 species, has recently been published by Seagrief (1984). But it is certain that undescribed taxa and new records remain to be reported for this richly diversified coastline, affected by both the warm-water Agulhas Current and the cold-water Benguela Current (Branch and Branch 1981). One such example is an apparent new species of the red algal genus *Neoholmesia* (Delesseriaceae). The purpose of this paper is to describe this alga and to present some information on its relationship to *Holmesia capensis* J. Agardh, *Heteroglossum*, and other species of *Neoholmesia*.

Materials used in the Present Study

Collections of the new species were made at two sites on the Natal coast of South Africa, and the specimens were preserved in 5% formalin/sea-water. The material was washed and then stained with a mixture of very dilute (less than 1%) aniline blue acidified with HCl and also containing 30% liquid glucose (Karo syrup). Drops of 50% Karo syrup were added to the edge of the cover-slip until the mounted specimen became solidified. A Zeiss research microscope equipped with a standard camera-back and also with a *camera lucida* was used in making observations. Specimens have been deposited in the herbaria of the University of Natal, Pietermaritzburg (NU), and the University of Michigan, Ann Arbor (MICH).

Observations

a) Vegetative structure

The thalli (Figs 5, 9, 10, 13) consist of a basal portion of terete, cartilaginous axes, usually 2 to 4 mm in diam., that are firmly attached to rock substratum at the lowest tidal level, and upper portions of delicate blades. These terete axes in cross-section (Fig. 4) have an organization of a mixture of large and small cells in the medulla and a zone of small, pigmented cortical cells at the periphery.

Individual blades grow by means of a transversely dividing apical cell, which cuts off segments proximally, making up the primary axial row (Fig. 1). Each of these primary segments cuts off a ring of four pericentral cells, of which a pair of lateral pericentral cells contributes to the formation of the wings of the blade. These wings, or "alae", are the product of the congenital fusion of the edges of the second-order cell rows along with the third-order (or higher) cell rows. No intercalary cell divisions occur in this process. Only the initials of the various orders of cell rows undergo division. Not all of the 3rd-order initials reach the thallus margin. This apical organi-

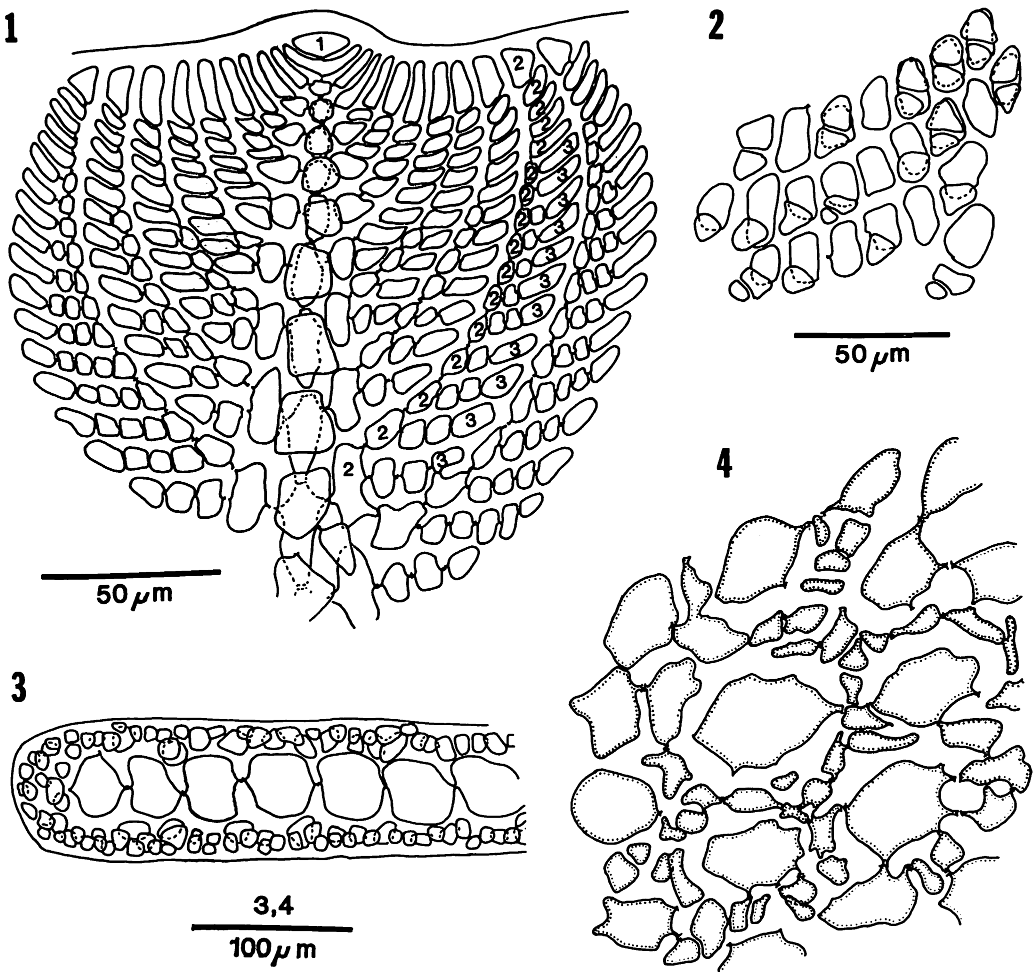
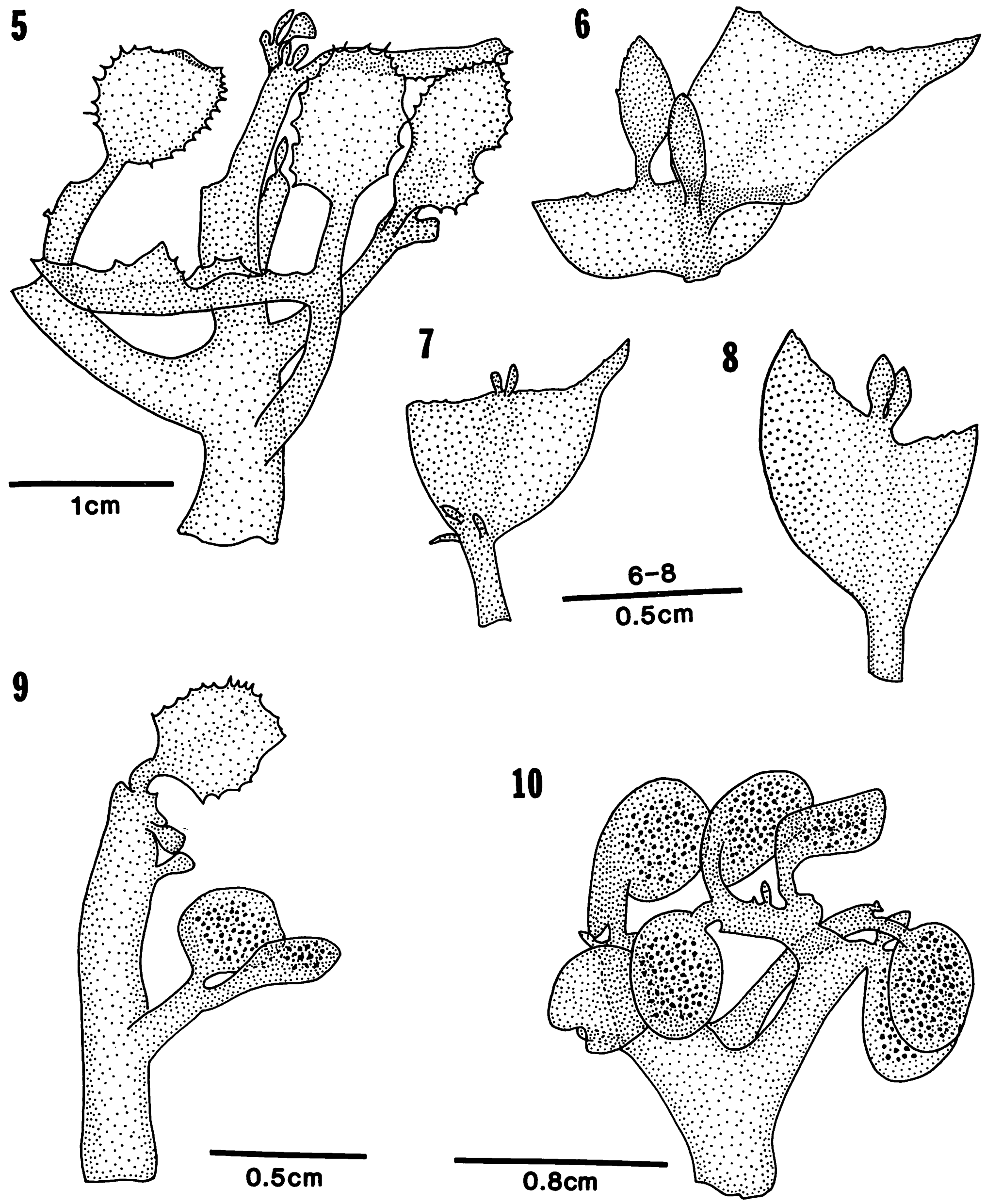


Fig. 1-4. *Neoholmesia natalensis*. Fig. 1. Apex of blade showing organization conforming to Membranoptera-type. *1*, primary apical cell; *2*, cell of 2nd-order row; *3*, initials of 3rd-order row. Fig. 2. Initiation of cortical layer from cells of primary layer. Fig. 3. Cross-section of portion of blade near margin. Fig. 4. Medulla of terete axis in cross-section, showing intermixed large and small cells.

zation (Fig. 1) conforms to the Membranoptera-type (Kylin 1924).

Although the blade is monostromatic near its distal end and along its growing margins, there is soon developed a cortical layer on both surfaces of the blade. These cortical cells are produced by small cells being budded off the corners of the primary layer of cells (Fig. 2). These new superficial cells continue growth by further division, eventually producing a continuous layer of cortical cells covering the primary layer of larger



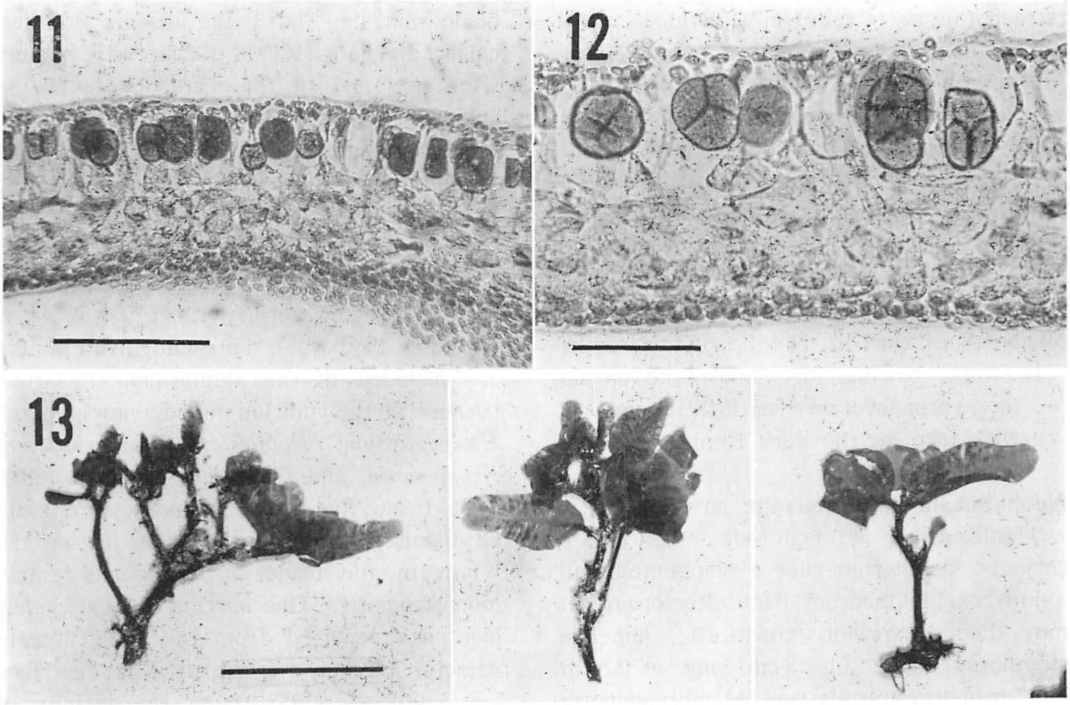
Figs 5-10. *Neoholmesia natalensis*. Fig. 5. Thallus with new blades from basal terete axes. Figs 6-8. Proliferation of new blades from near the midlines of damaged blades. Figs 9-10. Tetrasporangiate blades.

cells. A polystromatic blade is developed (Fig. 3). The blade is thicker along its midline, although a midrib is not conspicuously defined.

Margins of the blades may be perfectly entire (Fig. 9), or they may be serrate (Figs. 5, 10). No instances of branches arising from the margins of blades were observed. With age, the lamina of the blades is eroded, leaving a thickened midline. This persistent midline is converted into the cartilaginous lower axes of the plant. New blades arise from these basal axes. With the repetition of the process, the axes become branched and further thickened. Some blades that were damaged had produced new blades from the midrib region immediately adjacent to the injury (Figs 6-8).

b) Production of tetrasporangia

Tetrasporangia are produced in a single layer on the adaxial surface of blades (Fig. 11) which arise from the cartilaginous axes in the same manner as new vegetative blades. The sporangial primordia are cut off laterally from columnar sub-cortical cells (Fig. 12). The sorus in longitudinal section assumes a palisade-like aspect because of the elongate cells that bear the tetrasporangia. Although the fertile blades are relatively small (Figs 9, 10) and do not reach the size of some vegetative blades, these tetrasporic blades are regarded not as special fertile proliferations (which would relate this alga to *Holmesia*) but as ordinary blades, relating this alga to *Neoholmesia*. The justification for this particular tenet is that they arise in a similar manner as ordinary sterile blades. There is nothing to distinguish them from non-fertile blades other than the presence of tetrasporangia. The tetrasporangia are tetrahedrally divided (Fig. 12). They reach a diameter of up to 50 μm at maturity.



Figs 11-13. *Neoholmesia natalensis*. Fig. 11. Cross-section of tetrasporangiate blade. Fig. 12. Detail of sorus, with tetrasporangia formed laterally from elongate cortical cells. Fig. 13. Herbarium specimens (NAT-1419 in NU). Scale bar; Fig. 11=100 μm; Fig. 12=50 μm; Fig. 13=2 cm.

Diagnosis

Neoholmesia natalensis sp. nov.

Thalli to 4 cm in height, saxicolous, consisting of a cluster of blades arising from a basal system of branched, well developed cartilaginous axes 2–4 mm in diam.; individual blades to 1.3 cm long and 0.8 cm wide; apical organization of the Membranoptera type (that is, intercalary cell divisions lacking); blades becoming polystromatic, with a thickness of 125–130 μm away from the midrib; midrib of blade only vaguely evident; blade margin either entire or serrate; lamina of blades eroding with age, and the central portion persisting as thickened perennating axes, from which both new vegetative and tetrasporic blades arise; new blades also proliferating from the mid-region of damaged blades and from the basal portion of a blade but otherwise not arising from blade margins; tetrasporangia produced in a single layer on the adaxial surface of young blades arising from the thickened axes; tetrasporangia from the sides of columnar cells in a sorus; tetrasporangia tetrahedrally divided, 36–50 μm in diam.; sexual plants unknown.

Holotype: NAT-741, deposited in NU; collected by Bruce Emanuel, 9 May, 1982, Palm Beach, Natal, South Africa; tetrasporic.

Isotype deposited in MICH.

Other collection: NAT-1419, deposited in NU and MICH; collected by Mark Aken, 9 Sept., 1983, Rocky Bay, Park Rynie, south of Durban, Natal, S. Afr.; sterile.

Habitat: growing just below the spring low-water level on a south-facing vertical rock face (at the Park Rynie site).

Neoholmesia natalensis sp. nov.

Thalli usque ad 4 cm alt., saxicoli, e corymbo lamellarum quae e systemate basali axium cartilagineorum bene effectorum 2–4 mm diam. exorient constituti; lamellae singulares usque ad 1.3 cm long. et 0.8 cm lat., ordinatio apicalis typi Membranopterae (id est divisions intercalares cellularum nullae); lamellae polystromaticae (tristromaticae) 125–130 μm crass. de costa; costa lamellae vix manifesta, margo lamellae aut integer aut serratus, lamina lamellarum aetate erosa, et pars centralis ut axes incrassati perennantes persistens, e his axibus lamellae et vegetativae novae et tetrasporicae exorient; lamellae novae necnon e regione media lamellarum laesarum et e parte basali lamellae proliferentes, aliter, autem, e marginibus lamellarum non exorientes; tetrasporangia in strato unico in superficie adaxiali lamellarum iuvenium, ex axe incrassato exorientum, effecta; tetrasporangia e lateribus cellularum columnarium in soro, tetrasporangia tetrahedraliter divisa, 36–40 μm diam.; plantae sexuales ignotae.

Holotypus: NAT-741 (in NU)

Discussion

The members of the Membranoptera Group of the family Delesseriaceae are characterized by: 1) growth from a single transversely dividing apical cell; 2) not all of the initials of the third-order cell rows reaching the blade margin; and 3) the absence of intercalary divisions (KYLIN 1924). Five genera were assigned to this category by KYLIN (1956), but two of these genera were subsequently removed. *Microrhinus* was demonstrated to have intercalary divisions occurring in the second-order cell rows and was transferred to the Delesseria Group (WYNNE 1982). *Cyclospora* was shown to be ceramiacean and congeneric with *Carpoblepharis* (WYNNE 1985). At present five genera are included in the Membranoptera Group because of the addition of some new genera: *Heteroglossum, Holmesia, Membranoptera, Neoholmesia,* and *Pantoneura* (WYNNE 1983).

Of these five genera *Membranoptera* can be dismissed from consideration in that the wings of the blades in that genus remain monostromatic. One species of that genus has been reported from the Indian Ocean, namely, *M. murrayi*, which was described by BØRGESEN (1933) from the vicinity of Karachi, Pakistan. That alga has blades reaching 12 cm in height but only to 2 mm in width. Its delicate, much branched axes with their apparently monostromatic wings present a very different aspect than that of the South African alga under discussion. *Pantoneura* can also be ruled out on the basis of its vegetative branching being restricted to marginal outgrowths.

The remaining three genera must all be considered. It is questionable whether *Heteroglossum* actually belongs to the Membranoptera Group. When the genus was described, ZINOVA (1972) stated that it had an apex of the Membranoptera type, although she did not illustrate the apical organization. More recently, PERESTENKO (1983) merged *Yamadaphycus* (of MIKAMI 1973) into *Heteroglossum*. Since *Yamadaphycus* had been shown by Mikami to have an apex of the Delesseria type (i.e., with intercalary divisions occurring in the second-order cell rows), it is implied by Perestenko's merger that she must have found *Heteroglossum* to also have a Delesseria-type apex, contrary to Zinova's original characterization.

The holotype of *Heteroglossum ochotense* was borrowed from LE and examined. This specimen was figured by ZINOVA (1972, fig. 3). It was not possible for me to determine whether the apex conforms to the Membranoptera- or the Delesseria-type. Cortication commences very close to the apex, making it difficult to observe the possible occurrence of intercalary cell divisions in the second-order cell rows. The apex did not present the very regular pattern seen in *Neoholmesia natalensis* (Fig. 1). Tetrasporangia are produced on a variety of ligulate and ciliform proliferations that arise from all over the blade surface and the margins. I did not observe tetrasporangia on the larger primary blade surfaces. If the apex of *H. ochotense* indeed is of the Delesseria-type, then it can be dismissed from further comparison with *Neoholmesia natalensis*. On the other hand, if *H. ochotense* does properly belong to the Membranoptera Group, it is still possible to differentiate it from the South African alga by the strong midrib and the production of proliferations from the margins and randomly over the blade surface in *Heteroglossum* (ZINOVA 1972).

Holmesia, as typified by *H. capensis* J. AGARDH (1890), is known from the east coast of South Africa in the area of Port Alfred and East London (WAGNER, 1954). A specimen in MICH (W. TYSON "South African Marine Algae No. 125") is an alga with a much branched thallus consisting of ligulate blades 18 cm in length and to 2 cm in width; the branches arise both from the blade margins and from the poorly defined midrib. Tetrasporangia occur in special proliferations, each about 1 mm long, that arise in clusters randomly grouped on both surfaces of the blade. Both the physical dimensions of this species and the manner of tetrasporangial production are in disagreement with the alga under discussion from Natal.

Another species of *Holmesia* is *H. californica* (DAWS.) DAWS., which seems to be of rare occurrence but of wide range on the coast of Pacific North America (ABBOTT and HOLLENBERG 1976). This species was first described as an alleged parasite (*Loranthophycus californicus*) by DAWSON (1944), but he soon realized that this so-called "parasite" merely represented the special (tetrasporic) proliferations occurring on the primary blade, which is characteristic of the genus *Holmesia* (DAWSON 1945). On the basis of present evidence there seems no reason to question the placement of this species in *Holmesia*.

With *Membranoptera*, *Pantoneura*, *Heteroglossum*, and *Holmesia* all eliminated from consideration, only *Neoholmesia* remains of the genera of the Membranoptera Group. The evidence generally supports the assignment of the Natal alga to this genus. *Neoholmesia* was established by MIKAMI (1972) for an alga occurring in northern Japan and first described as *Botryocarpa japonica* by OKAMURA (1910). Recognizing that the apex of this species had the organization of the *Membranoptera* type, OKAMURA (1932) subsequently transferred this species to *Holmesia*. MIKAMI (1970, 1972) later observed tetrasporic plants for this species and saw that the tetrasporangia are scattered randomly over the surfaces of the blade rather than being confined to special fertile proliferations as in the type of the genus, *H. capensis* (WAGNER 1954). MIKAMI thus established *Neoholmesia* on this difference in regard to tetrasporic plants and also on the basis of the carposporangia being borne in chains rather than terminally as in *H. capensis*.

Only one other species has so far been assigned to *Neoholmesia*, namely, *N. triangulata* (ZIN.) ZIN. This species was first described as *Sachalinella triangulata* by ZINOVA (1972), the type of a new genus. ZINOVA (1976) later conceded that her alga was congeneric with MIKAMI's *Neoholmesia*, the latter having priority by two months. Although ZINOVA expressed the opinion that *Neoholmesia* and *Sachalinella* were congeneric, she regarded her species as different from the type of *Neoholmesia* and thus made the combination *N. triangulata* (ZINOVA 1976). Although both species were described from Sakhalin Island (Soviet Union), thalli of *N. japonica* have basically a single order of branches and the blades are relatively smooth in texture, whereas thalli of *N. triangulata* have blades arising in groups of four to eight, representing a second order of branching, and the blades are rough (squarrose) in texture. In both species blade margins range in appearance from smooth to coarsely serrate or dentate. Lateral veins are absent. A midrib is vaguely present in the lower portion of the blade but fades distally. The thickened midline of the primary blade remains after the lamina is eroded, and the higher order of branches arises from this axis.

Perhaps the most significant point of difference in the South African alga from *Neoholmesia* is the fact that the tetrasporangia are borne in a single subcortical layer on the adaxial surface of the blade. In *N. japonica* the tetrasporangia are produced in sori on both surfaces of the main thallus (MIKAMI 1970). Indeed, in almost all known members of the Delesseriaceae tetrasporangia are formed in two layers, that is, one layer on each surface of the blade. The only exceptions to this pattern are the following: a single, central layer of tetrasporangia in *Taenioma*, *Caloglossa*, and the Sarcomenieae (PAPENFUSS 1944, 1961; WOMERSLEY and SHEPLEY 1959; WYNNE and KRAFT 1985); stichidia formation in such genera as *Zinovaea* and *Kurogia* (WYNNE 1983); and tetrasporangia in several layers, such as in *Vanvoorstia* and *Neohypophyllum* (PAPENFUSS 1937; OKAMURA 1922). Thus, the production of tetrasporangia in a single subcortical layer (Fig. 11) as seen in this new species from South Africa is an apparently unique feature and may indicate grounds for generic recognition. In the absence of sexual plants, however, it seems prudent to assign it to the most closely related genus, namely, *Neoholmesia*.

Another alga that had been placed in *Holmesia* deserves some attention. *Holmesia neurymenioides* (OKAM.) OKAM. was first described as a *Botryocarpa* by OKAMURA (1929) and was later transferred to *Holmesia* (OKAMURA 1932). This speciesw as recorded from Taiwan and apparently has not been re-collected since its discovery (Y. M. CHIANG *in litt.*,). OKAMURA (1929) described the tetrasporangia in this species as being scattered over the surfaces of the blades, thus in agreement with the arrangement in *Neoholmesia* and not as in *Holmesia*. The species was not referred to by MIKAMI (1972). On the basis of its tetrasporangial arrangement this species should be transferred to *Neoholmesia*:

Neoholmesia neurymenioides (OKAMURA) comb. nov.

Basionym: *Botryocarpa neurymenioides* OKAMURA, 1929, p. 11, pl. 257.

Synonym: *Holmesia neurymenioides* OKAM.) OKAM., 1932, p. 98.

In conclusion, the following species of *Neoholmesia*, with their places of occurrence, are recognized:

1) *N. japonica* (OKAM.) MIKAMI, the type of the genus: Sakhalin Island, Soviet Union; Korea (KANG, 1966)

2) *N. triangulata* (A. ZIN.) A. ZIN: Sakhalin Island, Soviet Union
3) *N. neurymenioides* (OKAM.) Wynne: Taiwan
4) *N. natalensis* Wynne: south and central coast of Natal Province, South Africa

The striking regularity of the cell rows, resulting from the lack of intercalary divisions, is a feature of these algae. This pattern observed in *N. natalensis* (Fig. 1) can be compared with that figured for *N. japonica* by MIKAMI (1972, fig. 1) and for *N. triangulata* by ZINOVA (1972, fig. 2-1). The variable appearance of the blade margin (smooth or serrate) noted for *N. natalensis* has also been described for *N. neurymenioides* by OKAMURA (1929, pl. 257), in which they were referred to as "entire or fimbriate". The blades of *N. triangulata* were reported to have serrate margins (ZINOVA 1972), and those of *N. japonica* were reported to have coarsely dentate margins (OKAMURA 1910).

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ウイン, M. J.: 南アフリカ産コノハノリ科の1新種 *Neoholmesia natalensis*

南アフリカ共和国ナタールの Park Rynie と Palm Beach の海岸からコノハノリ科の1新種 *Neoholmesia natalensis* ナタールスズシロノリが記載された。本種の生長点構造は，本種が Membranoptera グループに所属することを示し，体は polystromatic になる。葉状体の中肋部は厚くなり，軟骨質の軸となり存続する。この軸から新しい小葉が発出してくる。四分胞子嚢はこれらの厚くなった軸から生じている小葉の上に形成される。四分胞子嚢を生じている小葉は，同じ方法で生じてくる vegetative な小葉と区別がつかない。よく発達した多年生軸からなる基部組織と，小葉の向軸側面の表皮細胞に限って四分胞子嚢を生じることは，この種の特徴的形質である。また新しい組み合わせ *Neoholmesia neurymenioides* (OKAMURA) WYNNE が提案された。