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Peter Saenger
Southern Cross University

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ON THE OCCURRENCE OF *OPHIDOCLADUS* (RHODOMELACEAE) IN SOUTHERN AFRICA

P. SAENGER

(*Department of Botany and Microbiology, Rhodes University, Grahamstown, South Africa*)

ABSTRACT

Collections of *Ophidocladus* (Rhodomelaceae) from Moçambique and South Africa were studied and the relationship of this material with the type species (*O. simpliciusculus* (Crouan) Falkbg.) and other related taxa, is discussed in detail. Based on the vegetative and reproductive uniformity, it is concluded that the material of *Ophidocladus* from Europe, Southern Africa, Western Australia, North and South America is best included in the type and only species. Hence *O. californica* (Hollenberg) Kylin and *O. herposiphonioides* Joly et Yamaguishi are reduced to synonomy. A map showing the known distribution of *Ophidocladus* is given.

UITTREKSEL

DIE VERSPREIDING VAN *OPHIDOCLADUS* (RODOMELACEAE) IN SUIDLIKE AFRIKA.

Versamelings van *Ophidocladus* (Rhodomelaceae) uit Mosambiek en Suid-Afrika is bestudeer en die verwantskap tussen hierdie monsters en die tipe spesies (*O. simpliciusculus* (Crouan) Falkenberg), asook ander verwante taksa, is volledig bespreek. Op grond van die eenvormigheid van die vegetatiewe en voortplantingsstrukture, word dit afgelei dat die plante van *Ophidocladus* uit Europa, suiderlike Afrika, Wes-Australië, Noord- en Suid-Amerika by die tipe en enigste spesies hoort. Dus word *O. californica* (Hollenberg) Kylin en *O. herposiphonioides* Joly et Yamaguishi 'n sinoniem onder *O. simpliciusculus* verlaag. 'n Kaart word voorsien waarop die verspreiding van *Ophidocladus* aangegee word.

INTRODUCTION

While describing another rhodomelaceous alga, Pocock (1953: 43) mentions the occurrence of an undetermined species of *Ophidocladus* at Muizenberg, Cape Province, South Africa and an identical alga was subsequently recorded from Inhaca Island, Moçambique (Pocock, 1958). Since the nearest records of *Ophidocladus* are from the Canary Islands (Børgesen, 1930) and Western Australia (Falkenberg, 1901), a study of the southern African material was made in order to determine its relationship to the type species *Ophidocladus simpliciusculus* (Crouan) Falkenberg. In addition to the type species, the southern African material was also compared with the related *Ophidocladus californica* (Hollenberg) Kylin from the Californian coast, *Ophidocladus herposiphonioides* Joly et Yamaguishi from Brazil and *Polysiphonia obscura* Harvey from Western Australia. Other collections of *Ophidocladus* from southern African localities were also examined and the findings are given.

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Material Examined

Type specimen—*Ophidocladus simpliciusculus* (Crouan) Falkenberg. Ex Herb. Crouan, Algues marines du Finistère, No. 302. (Now in PM—unnumbered.)

South Africa —Strandfontein, 19.ix.40 (Pocock, 3299)*.
Kasouga, 11.vi.44 (Pocock, 8165).
Cannon Rocks, Richmond, 23.x.44 (Pocock, 8223).
Muizenberg, 7.xii.45 (Pocock, 8568); 14.xii.51 (Pocock, 10200).
Sedgefield, 20.viii.51 (Pocock, 9317).
St. James, 19.xii.51 (Pocock, 10261).
Swartklip, 1.i.52 (Pocock, 10259).
Platboom, 14.i.52 (Pocock, 10294).
Kowie, Salt Vlei, 21.iv.60 (Pocock, 13965).
Kowie, Shark Bay, 21.iv.60 (Pocock, 13960).

Moçambique —Inhaca Island, 26.ix.57 (Pocock, 12162); 30.i.71 (Saenger, 594).

United States —Corona del Mar, California, 24.x.42 (Hollenberg, 3286).

Australia —King George's Sound (Harvey, TCD 182-B) (Annotated in Harvey's handwriting: "*P. simpliciuscula* Cr. fida. J. Ag. *P. obscura* Harv. (nec. Ag.)".
—King George's Sound (Harvey, TCD—unnumbered: annotated 'KGS' in Harvey's handwriting in addition to 'cf *Polysiphonia obscura*').

Unfortunately no herbarium specimens of *O. herposiphonioides* from Brazil were available and all comments and measurements are based on the descriptions and illustrations in Joly (1965) and Joly *et al.* (1963).

Generic Limits of *Ophidocladus* Falkenberg (1897)

The genus *Ophidocladus* was described by Falkenberg (1897) from a Crouan specimen of *Polysiphonia simpliciuscula*. According to Falkenberg, *Ophidocladus* is characterised by its peculiar thallus structure, consisting of an erect and prostrate system. The prostrate system is attached to the substratum by unicellular rhizoids and possesses 10—20 pericentral cells. It is dorsiventrally organized with the first pericentral cell cut off in a single dorsal row. No cortex is formed and trichoblasts are absent. This prostrate system gives rise to a number of dorsally inserted, endogenous erect brancbes, which, although lacking a cortex, do form trichoblasts alternating in two diametrically opposed rows. In contrast with the dorsiventral system, the erect branches are radially organised with a 1/2 divergence between successive trichoblasts.

* (All MAP specimens now housed in Albany Museum Herbarium (GRA)).

With the exception of the trichoblasts and the unicellular rhizoids, all branching is endogenous. In general, two tetrasporangia are produced in each fertile segment.

Another species (?*Ophidocladus schousboei* (Thuret) Falkenberg) provisionally placed in *Ophidocladus* by Falkenberg (1901) has subsequently been removed and placed in a separate genus *Leptosiphonia* as *L. schousboei* (Thuret) Kylin (1956: 509). The latter genus is readily distinguished from *Ophidocladus* by the exogenous branching of the fronds and the absence of a dorsiventral prostrate system.

Description of the Southern African Plants

A. Gross morphology

The fronds vary in height from a few millimetres to approximately 4 cm and generally form dense, extensive mats on sand-swept rocks in the lower littoral zone.

The prostrate system is attached to the substratum by a number of unicellular rhizoids issuing from the ventrally situated pericentral cells. The apices of the prostrate branches are curved towards the substratum (Figure 1) and produce 15—25 pericentral cells.

On the dorsal side of the prostrate system, erect branches arise endogenously at more or less regular intervals (3—6 segments, Figure 1). At first, these are curved towards the tip of the prostrate branches but they later become straight.

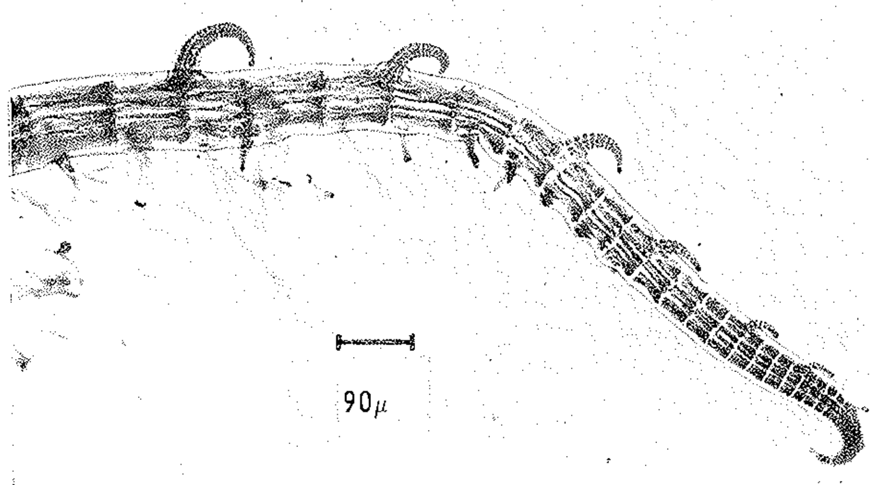

Fig. 1.
Apex of prostrate branch showing ventrally curved tip and the initiation of ventral rhizoids and dorsal endogenous erect branches.

In both prostrate and erect branches, there are 15—25 pericentral cells and no cortex is formed. At the apices of the erect branches, distichously inserted trichoblasts are produced.

Between successive erect branches, the prostrate branches produce paired lateral branches from one of the segments, eventually developing into new prostrate systems. Often only one of the pair develops into an indeterminate prostrate branch while the other remains only a few segments in length.

B. Apical segmentation

Segmentation of the prostrate branches occurs from a dome-shaped apical cell. The first pericentral cell of each segment is cut off dorsally and directly above that of the previous segment. The remaining pericentral cells then form

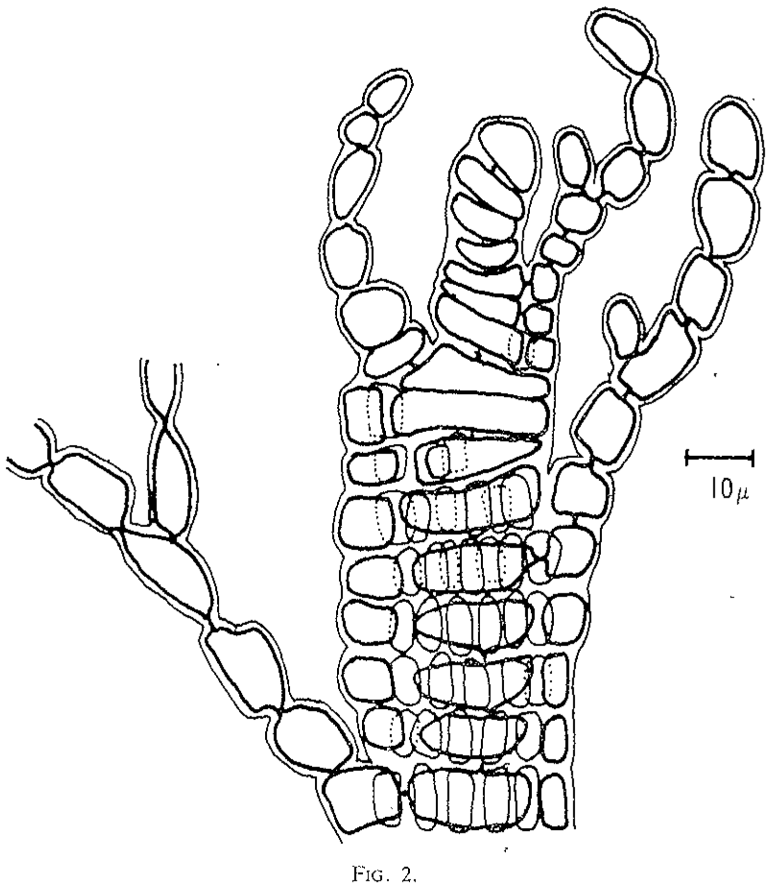

Fig. 2.

Apex of erect branch bearing alternate-distichously inserted trichoblasts. Note the formation of the first pericentral cell immediately below each trichoblast.

in an alternating sequence as generally found in the Rhodomelaceae. The endogenous erect branches emerge immediately in front of the first pericentral cell of that segment of the prostrate branch and consequently the erect branches are also produced in a single dorsal row (Figure 1).

Development of the erect branches proceeds by means of a dome-shaped apical cell forming discoid segmental cells. Every third or fourth segmental division is oblique and gives rise to a trichoblast initial (Figure 2). The trichoblasts are dichotomously branched, colourless and deciduous. The first pericentral cell of the erect branch is cut off immediately below the point of insertion of the trichoblast (Figure 2) and the remaining pericentral cells are then formed first to the left when viewed from above and then to the right and so forth until 15—25 pericentral cells have been formed in each segment. As the arrangement of the trichoblasts on the erect branches is alternate-distichous, the erect branches are radially organized with a 1/2 divergence between successive trichoblasts.

C. Branching

With the exception of the trichoblasts and the unicellular rhizoids, all branching is endogenous. From the prostrate system, dorsal endogenous erect branches are regularly initiated every 3—6 segments and thus constitute ordinary ('normal') endogenous branches. As the paired lateral prostrate branches also occur regularly between two successive erect branches, these paired laterals must also be considered as ordinary, endogenous branches. However, in older parts of the prostrate system, some adventitious, endogenous laterals are also formed and, together with the degeneration of some of the paired laterals, are responsible for the irregular appearance of the older parts of the prostrate system.

In the erect branches, all polysiphonous laterals are endogenous and mostly ordinary in origin. These laterals develop either from the trichoblast-bearing segment or from the segmental cell immediately below that bearing (or formerly bearing) a trichoblast (Figure 3). The first cell of the polysiphonous lateral emerges between the pericentral cells on that side where the trichoblast is (was) situated (Figure 3), resulting in the polysiphonous lateral being borne on the same side of the axis as the first pericentral cell of that segment (cf. Hommersand, 1963: 341). Hence, these laterals exhibit the same alternate-distichous arrangement as the trichoblasts. This type of branching represents ordinary endogeny (sensu Falkenberg, 1901; Saenger, 1970) since the polysiphonous laterals are directly related in their position to the ordinary, exogenous trichoblasts. Later in development, some adventitious endogenous branching of the erect branches also occurs, resulting in irregular branching of the mature fronds.

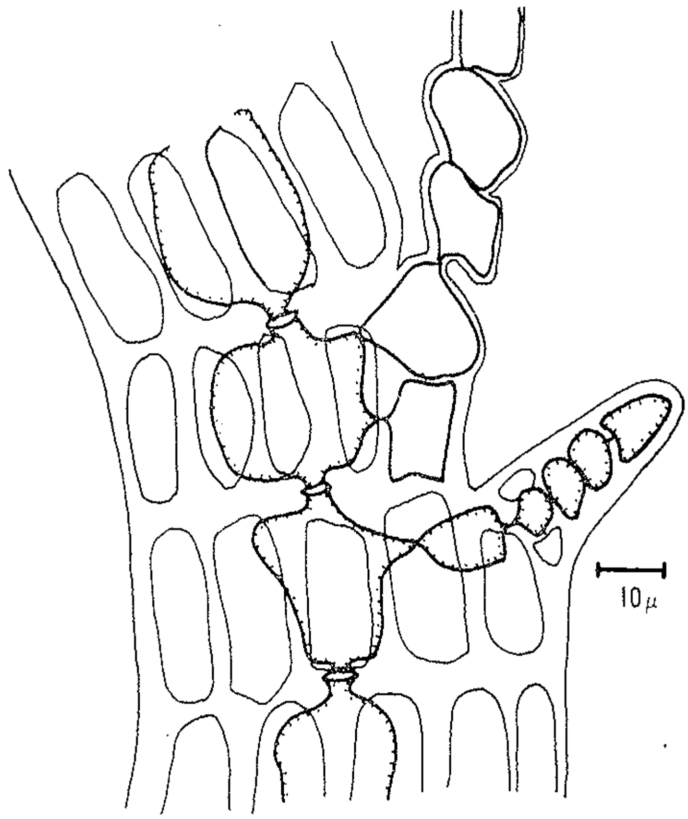

FIG. 3.
Production of an endogenous lateral from a segment immediately below that bearing a trichoblast.

D. Development of the procarp and cystocarp

Mature cystocarps generally develop only on cystocarpic plants but in several plants examined, such cystocarps were found on the tetrasporic plant (Figure 4).

The procarp always develops on a trichoblast and here, generally on the third segment (Figure 5). The basal segment of the procarpial trichoblast does not produce pericentral cells but the two following segments produce approx-mately 5—7 pericentral cells. One of the pericentral cells of the third segment acts as the supporting cell for the procarp and gives rise to one basal and 2 lateral sterile cells (Figure 5). A four-celled carpogonial branch is then formed from

FIG. 4.
Part of a tetrasporic plant bearing two lateral cystocarps on one of the lateral branches.

the supporting cell. The trichoblastic origin of the procarp can be seen by the continued monosiphonous growth of the trichoblast beyond the procarp (Figure 5).

Before fertilization, the pericarp is initiated by the repeated longitudinal divisions of the pericentral cells of the fertile segment and those immediately below it. No detailed observations were made on the processes of fertilization and gonimoblast formation. The mature cystocarp is globose to ovoid and more or less sessile (Figure 6). Remains of the sterile cells and a large fusion cell are present, the latter producing gonimoblast filaments bearing terminal carposporangia.

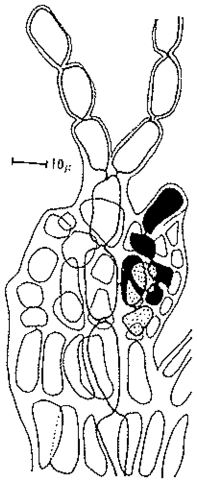

FIG. 5.

Trichoblast with fully developed procarp. Supporting cell and the carpogonial branch cells are black while the two lateral and one basal sterile cells are stippled.

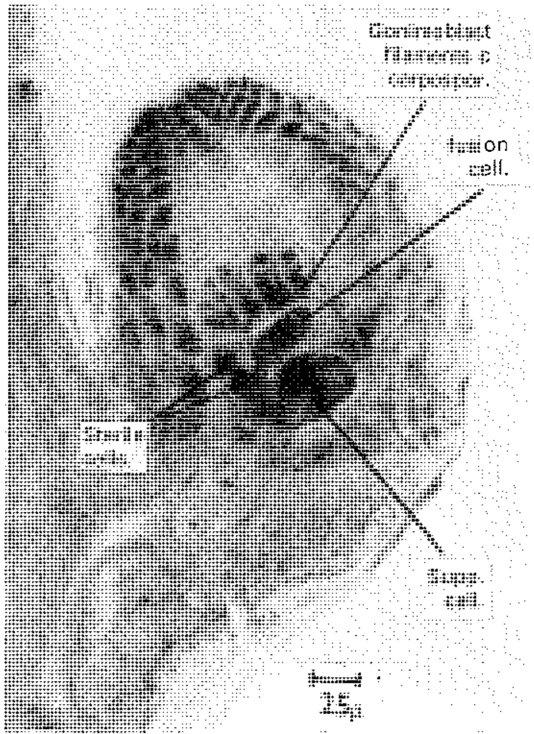

FIG. 6.

Optical section of a cystocarp showing large supporting cell, fusion cell, two sterile cells and short gonimoblast filaments with small immature carposporangia.

E. Development of spermatangia

Spermatangia are developed on the trichoblasts of the erect branches. These trichoblasts arise in an alternate-distichous manner (Figure 7a—e) at intervals of 2—5 segments. Like the sterile trichoblasts, the spermatangial trichoblasts are branched. While the basal segments form pericentral cells, the tips of the trichoblasts remain monosiphonous and free. Spermatangial mother cells are formed on the pericentral cells, each pericentral cell giving rise to 1—4 spermatangial mother cells. Between 2—8 spermatangia are then formed on each of the spermatangial mother cells. Overlapping of the spermatangial branchlets at the bases of the trichoblasts results in broad, cylindrical spermatangial branches measuring 60—300 μ in diameter (Figure 7e).

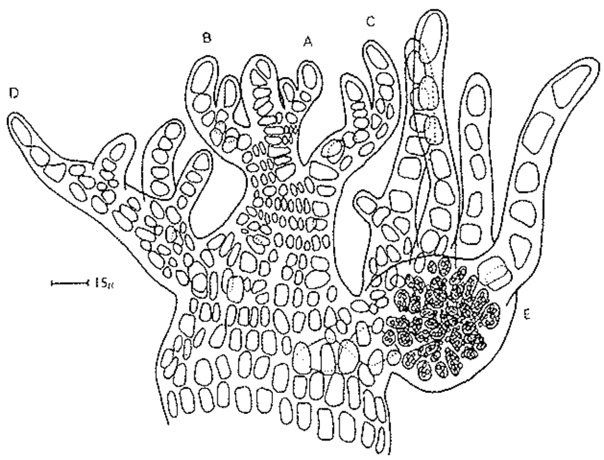

FIG. 7a—e.
Branch apex of male plant with developing spermatangial trichoblasts.

F. Development of tetrasporangia

Two tetrasporangia are usually produced per segment and are arranged in straight series in the terminal portions of the erect branches (Figure 4). The two sporangia lie in a plane perpendicular to the plane of insertion of the trichoblasts (cf. Hollenberg, 1943 fig. 11). Each fertile segment produces between 10—20 pericentral cells. The two fertile pericentral cells elongate radially and cut off two cover cells at their distal ends. The cover cells assume a size and shape identical to the sterile pericentral cells. No further division of the cover cells was observed. After cover cell formation, the sporangium is cut off in a median position on the pericentral cell. The tetrahedrally divided sporangium is 45—65 μ in diameter and is released through vertical slits between the sterile pericentral cells. It has not been possible to determine exactly which pericentral cells produce the tetrasporangia but since the first formed pericentral cells lie in a plane at right angles to the tetrasporangia, it is likely that the sporangia are formed from the seventh and eighth pericentral cells.

DISCUSSION

From the description given of the southern African plant, it can be seen that it readily agrees with the generic features of *Ophidocladus*. In 1943, Hollenberg described *Rhodosiphonia californica* from the Californian coast and separated this alga from *Ophidocladus* because of the manner of origin of the lateral branching. Hollenberg (1943) maintains that while *Ophidocladus* has ordinary, endogenous branching, *Rhodosiphonia* is characterized by adventitious, endogenous branching. Examination of the branching of *R. californica* showed it to be the same as in *O. simpliciusculus* from France and the African and Australian material. For reasons discussed earlier, this branching is considered ordinary although inconsistent development and later adventitious branching gives the appearance of an irregularly branched frond.

Falkenberg (1901) recognized that the lateral branches of the erect system of *O. simpliciusculus* were directly related to the position of the trichoblasts but he was inconsistent in his terminology. On p. 490, he states that "diese *Adventivsprosse** . . . nur von den blattbildenen Segmenten erzeugt werden und durch die Narbe des abgefallenen Blattes nach aussen treten." Yet on p. 55 of his work, Falkenberg states that as "die Stellung der . . . Sprosse gesetzmaessig geregelt ist, so muss man sie als *normale** Sprosse bezeichnen".

In addition to the ordinary laterals, truly adventitious laterals are formed later during development. It seems likely that the presence of both types of laterals led Hollenberg (1943) to conclude that the Californian alga differed from *Ophidocladus* in the manner of origin of the lateral branches.

Kylin (1956: 542) included the Californian plant in *Ophidocladus*, retaining it as a separate but closely related species because of its smaller size and sparser branching than in the type species.

Recently Joly *et al.* (1963) described *O. herposiphonioides* Joly et Yamaguishi from São Paula, Brazil. The habit of this plant with its prostrate and erect systems and the internal organization undoubtably confirm its inclusion in the genus *Ophidocladus* as previously defined. However from the descriptions and illustrations of this plant in Joly (1965) and Joly *et al.* (1963), there appears to be no valid reason for maintaining this alga as a species separate from *O. simpliciusculus* since the type and manner of branching and the formation of reproductive structures is identical to that found in *O. simpliciusculus* from other localities.

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* The italics are mine.

Comparisons of dimensions of certain features of the type specimen of *O. simpliciusculus* and specimens from California, Brazil, Moçambique, two South African localties and Western Australia (Table 1) shows the similarity of all the material. The internal organization of all the plants is identical and the dimensional variation between the specimens is no greater than that found in material from any one localtiy. In addition, the characteristic transverse banding of the cytoplasm of *O. californica* (Hollenberg, 1943) is also present in the southern African material and a re-examination of the type and Western Australian specimens, showed it in these plants as well. On occasions, three tetrasporangia are formed in the fertile segments of *O. californica* (Hollenberg, 1943) and similar occurrences were noted in the South African material.

TABLE 1

Comparison of dimensional data of *Ophidocladus* from a number of localities with the type specimen.

Character	*Ophidocladus simpliciusculus* TYPE	*Ophidocladus*					
		California	Muizenberg	Salt Vlei	Moçambique	Western Australia	Brazil*
Frond height (cm)	1—3	1—3	2—4	1—2	2—3	2—4	3—6
Branch diam. (μ)	100—150	80—140	90—200	90—150	100—160	100—150	100—180
Number of pericentral cells	12—20	14—20	15—25	15—18	16—18	12—22	17—27
Length/diameter of segments	0,7—1,0	0,7—1,0	0,6—1,3	0,5—1,3	0,6—1,0	0,7—1,1	0,8—1,6
Diameter of tetraspores (μ)	—	40—60	45—65	40—65	45—70	40—60	40—60
Diameter cystocarps (μ)	—	250—300	350—400	—	—	—	—
Diameter of spermatangial branches (μ)	—	90—300	60—300	—	—	—	150

* Data from Joly (1965) and Joly *et al.* (1963).

The separation of the Californian plant from the type species appears to be based on an incomplete analysis of the branching type and on trivial vegetative features such as size and density of branching. For some time the Australian specimens of *Ophidocladus* were considered as belonging to a separate species because of their geographical isolation (Falkenberg, 1901; Kylin, 1956). Other authors (Harvey, 1863; xxii; Børgesen, 1930; Lucas and Perrin, 1943; May, 1965) have included the Australian alga with *O. simpliciusculus* and comparisons with the other plants (Table 1) supports such an inclusion.

As the southern African material covers the whole range of vegetative variation and, as the reproductive structures are identical in all the material examined, it appears best to include all the plants presently placed in *Ophidocladus* in the type and only species.

NOMENCLATURE AND DISTRIBUTION

Based on the findings given above, the following synonomy applies: *Ophidocladus simpliciusculus* (Crouan) Falkenberg 1897: 461.

Basionym—*Polysiphonia simpliciuscula* Crouan 1867: 157 (Dried specimens were distributed under this name in "Algues marines du Finistère, Fasc. I–III' No. 302, Brest, 1852).

Synonyms—*Polysiphonia obscura* Harvey 1854: 541 (non *Polysiphonia obscura* (Ag.) J. Agardh 1842: 123 = *Lophosiphonia obscura* (Ag.) Falkenberg 1901: 500).
Polysiphonia corallioides Suhr in Kuetzing 1864: 18.
Rhodosiphonia californica Hollenberg 1943: 573.
Ophidocladus californica (Hollenberg) Kylin 1956: 542.
Ophidocladus herposiphonioides Joly et Yamaguishi in Joly, Cordeiro and Yamaguishi 1963: 60.

The distribution of *Ophidocladus simpliciusculus* and its various synonyms is given (Figure 8). All distribution records are in latitudes between 25°—45° both in the northern and southern hemispheres. No records from within the tropics are available. It seems probable that further search will locate *O. simpliciusculus* in other areas of similar latitudes.

Since completion of this manuscript, herbarium material of *O. herposiphonioides* (SPF 2750, Praia do Pouso, Municipio de Parati, Est. Rio de Janeiro, Brazil, 10th May 1963), kindly made available by Dr. E. C. de Oliveira Filho of the Botany Department, Sao Paulo University, has been examined and has confirmed the suggestions regarding its conspecificity with *O. simpliciusculus*.

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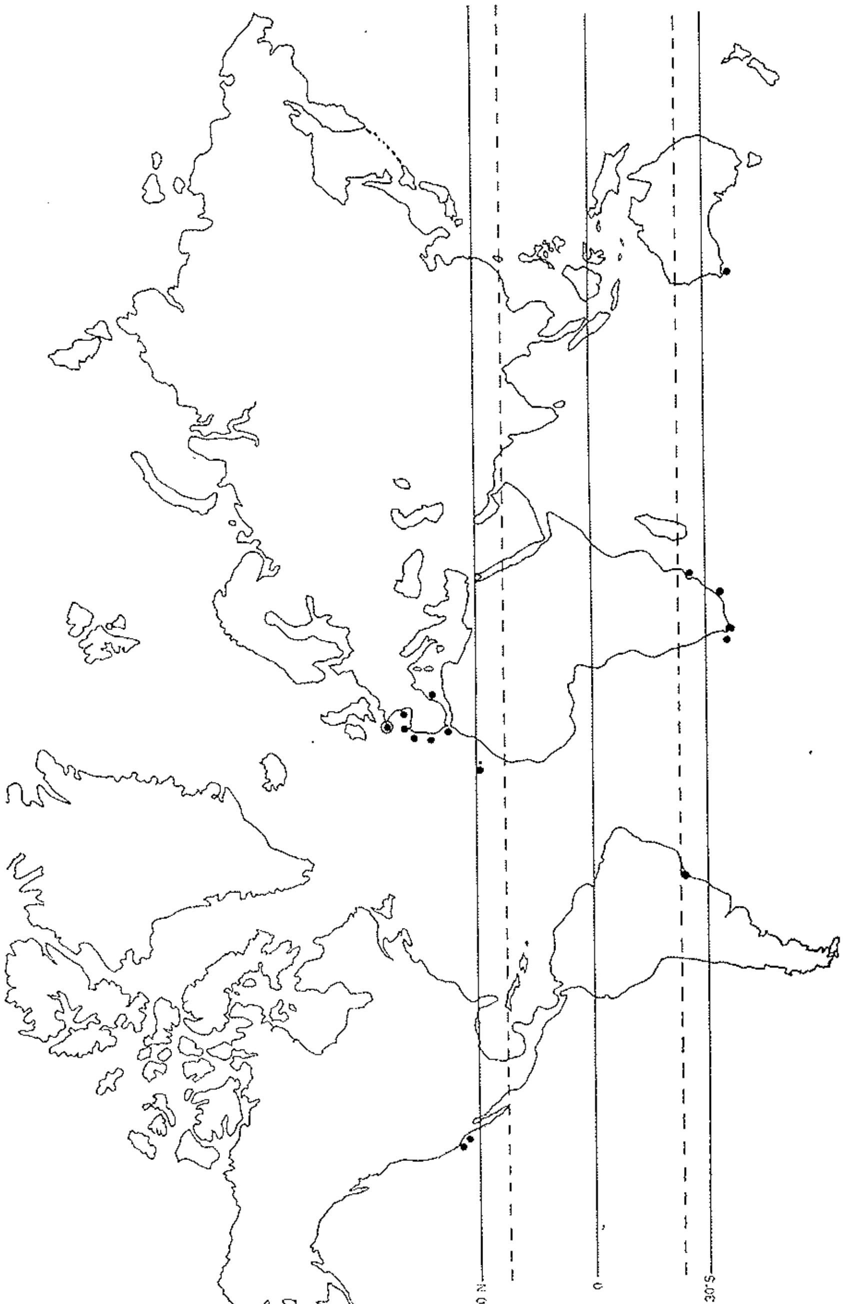

FIG. 8.
Map of world distribution of *Ophidocladus simpliciusculus*. The type locality is ringed.

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