NITELLA MADAGASCARIENSIS, NOV. SPEC., WITH NOTES ON THE CHAROPHYTA OF MADAGASCAR

by

J. S. ZANEVELD
(Rijksherbarium, Leiden)
(Issued June 15, 1939).

Our knowledge of the Charophyta of Madagascar is mainly based on the rich and well-prepared collection made by Mr Th. B. Blow, who visited the eastern central part of the island in the early months of 1924¹). The 384 dried specimens and a considerable number of portions of the plants preserved in formalin were determined by the well-known authority on the Charophyta, the late James Groves, who published the results of his work in the Journal of the Linnean Society (Botany), vol. XLVIII, 1928. This paper contains the descriptions of 5 new species and 3 new varieties of Nitella.

Before this basic paper on the Charophyta of Madagascar was published, only very few publications appeared. As far as I know the first Madagascan species to be recognized was "Chara ceylonica Willd." described by Bojer in the "Hortus Mauritianus" (1837, p. 427). The specimen was not seen by Braun, but he placed it in his large species C. gymnopus as subspecies C. Commersonii (1868, p. 872). Braun also states in the same work (l.c., p. 785) that he saw another specimen from Madagascar collected by Goudot, but did not mention it elsewhere in "Die Characeen Afrika's", nor has he cited the two specimens in his "Fragmente zu einer Monographie der Characeen" (1882). Though the latter work forms the starting point for the study of the Charophyta of almost every country all over the world, the name Madagascar is not to be found in it.

In a note to Baker's "Further contributions to the Flora of Madagascar" (1887) II. & J. Groves give the description of the first, and

¹) A brief account on the Charophyte collecting tours of Mr Blow is given by Allen (1938).
at the same time new *Nitella*-species from this island, named after his collector *N. Baronii*). After Groves's work in 1928 only one paper appeared containing notes on Madagascarian Charophytes, viz. part II of "New and noteworthy South African Charophyta" (1933) in which Groves and Miss Stephens describe two more new *Nitella*-species, collected already in 1879—'80 by J. M. Hildebrandt.

The present paper primarily deals with the description of a new *Nitella*-species, which was collected at the end of the foregoing year. Further a review in key-form of all described Charophyta of Madagascar is given, followed by a table with some additional remarks showing the geographical distribution and relationship. Finally some few general conclusions are drawn concerning the character of these species and the way in which they possibly entered Madagascar.

**Nitella madagascariensis, n. sp.**

(Figs. A—E)

*Latin diagnosis.*

*Planta* monoclea, alopecuroida, usque ad 7 cm alta, aeneovirescens. *Caulis* tenuissimus, ad 350 μ diam.; *internodia* in partibus inferioribus ramulis aequalibus, in partibus superioribus 1/4—2/3 ramulorum longitudinis. Verticillorum *ramuli steriles* normaliter 6, rigidi, e. 1 cm longi, 3—4-plo-furcati; radii primarii 2/3 totius longitudinis ramulorum; radii secundarii 3; radii tertiariorum 2—3 quorum saepe 1 in radios 2 quaternarios furcatae; omnes radii inaequales primariis exceptis; ramuli accessorii in omnibus verticillis. Verticillorum *ramuli fertiles* 6, conflerti, gymnocephali, e. 0.7 cm longi, 3-furcati; radii primarii dimidio longitudinis ramulorum breviores; radii secundarii 3—4; radii tertiariorum 2—3; radii quaternarii generatim 2. *Dactyli* ramulorum steriliae eis fertilibus similes, longitudine inaequalibus, 2—3-cellulati; cellula inferior elongata, apice trunca, obtuse emarginata, ad 150 μ diam.; cellula centralis 2/3 latitudinis inferioris, apice creata; cellula ultima conica, 60—100 μ longa, 30—45 μ lata, acutissima, saepe delapsa. ♂ et ♀ *gametangia* in omnibus nodis libris. *Antheridia* terminalia, plerumque solitaria rarissime geminata, plerumque brevior pedicellata vel subsessillia, e. 340 μ diam. *Oogonia* sessilia, lateralia, plerumque geminata, si solitaria antheridio

1) In consequence with the international rules I write "Baronii" instead of "Baroni".
conjuncta, constanter 500—510 μ longa (coronula incl.), 350—365 μ lata, cellulis spiralibus 7 (6—8), apices versus elongatis et bulbosis; coronula 75—90 μ alta, ad basin 65—80 μ lata; oosporae 275—325 μ longae, 270—295 μ latae, striis 6 (5—7); oosporae membrana translucens, pallide brunnea, anguloso-reticulata.

Description.

Plant monoeccious, bronze green, not more than 7 cm in height, with a fox-tail-like habitus, several branched stems rising from the same swollen node which is connected with other thickened nodes by means of colourless one-celled internodes, these swollen nodes and colourless internodes most probably forming together a kind of creeping rhizome. Stem very slender, up to 350 μ in diam.; internodes in the lower parts of the plant as long as the branchlets, in the upper parts 1/2—2/3 the length of the branchlets. Sterile branchlets usually 6 in a whorl, somewhat spreading and rigid, c. 1 cm long, twice and partially threecurrent; primary rays 2/5 the length of the entire branchlet; secondary

*Nitella madagascariensis* Zanev., nov. sp. —
A. habit, X c. 2; B. base of fertile whorl with one entire branchlet, X c. 12; C. immature oogonium showing the interstices for the penetrating spermatozooids, X c. 60; D. ripe oospore, X c. 55; E. part of the oospore membrane with decoration, X c. 460 (from the type material).
rays 3; tertiary rays 2—3 of which one is frequently again forked with 2 quaternary rays; all rays with exception of the primary are very unequal in length; the lower whorls only consisting of sterile branchlets; in nearly every whorl one new young, short shoot. Fertile branchlets usually 6 in a whorl, crowded, not enveloped in a mucous cloud, forming long dense, somewhat rigid plumes, 0.7 cm long; all branchlets thrice-furcate; primary rays shorter than half the length of the entire branchlet; secondary rays 3—4; tertiary rays 2—3; quaternary rays usually 2; all rays varying in length, especially the ultimate ones. 

Dactyls (ultimate rays) in the sterile and fertile branchlets 2—3, similar, very variable in length, 2—3-celled; basal cell much elongated, up to 150 μ in diam., truncate at apex and there with rounded margins; penultimate cell 1/3 the breadth of the basal cell, either very short or somewhat shorter than the basal one, truncate at apex; ultimate cell conical, at the base as wide as the penultimate cell, very acute, 60—100 μ long, 30—45 μ wide at base, very often broken off; the cell-lumen everywhere at the same distance from the outer part of the cell-wall, except at the top which shows a hyaline part. ♀ and ♂ gametangia present at all and at the same nodes, lacking at the base of the whorls; the younger fertile whorls, however, containing mainly antheridia. Antheridia solitary or very seldom geminate, sessile or short-stalked, terminal; on the younger whorls, however, apparently laterally inserted because they are pressed aside by the force of the young rays; c. 340 μ in diam. Oogonia frequently geminate, sometimes solitary, but then always together with an antheridium; laterally inserted at the nodes, especially at the lower ones; very constantly 500—510 μ long (incl. coronula), 350—365 μ wide with 7 (sometimes 6 or 8) broad spiral cells, which are very much elongated and swollen below the coronula, and at this spot showing interstices of c. 65 μ length and 20 μ width for the admission of the spermatozooids; coronula 75—90 μ high, 65—80 μ wide at base; in the mature oogonium the inferior series of cells less than half the length of the upper cells, c. 25 μ high, superior series of cells typical crown-like, individual cells diverging, c. 60 μ high; ripe oospore bright yellow brown, nearly globose, 275—325 μ long, 270—295 μ wide, with 6 (sometimes 5 or 7) prominent, broad striae; outer membrane very thin, translucent, tough, light yellow brown, angularly reticulate with a protuberance on each point of junction, showing about 10—12 meshes between the ridges.

Exsiccate.

Type collected in stagnant water in the vicinity of the Simianona-falls about 3 km west of Ambahaoabe, dist. Sonnerana, Madagascar, c. 40 m alt., by LAM.
and Meeuse, No. 5791, 6th December, 1938; dried and alcohol material in the Rijks-
herbarium, Leiden.

Lam & Meeuse No. 5792 is collected in a little tributary at about 1 km west
of Ambahoabe, same date, c. 35 m alt.; dried material only, in Rijksherh, Leiden.

Vernacular name: lomotra. This word, however, is also used
by the natives for mosses (cf. lumut, Malay).

Remarks.

Nitella madagascariensis is at first sight characterized by its fox-tail-
like habit (fig. A), particularly with regard to the specimens preserved in
fluid, and therefore it may be easily recognized in the field. The other
characteristics of the new species are the dactyls being partly two and
partly three-celled (fig. B), whereas only the ultimate cell has a nearly
uniform size. The spiral cells enveloping the oosphere are enormously
elongated just before fertilization, immediately below the lower cell-series
of the coronula (fig. C); by the force of this elongation the spiral cells
are opened at their apices, thus forming long channels serving for the
penetration of the spermatozoids. At this phase of development the upper
series of coronula cells forms a distinct crown by the divergency of the
individual cells. As soon as the oogonium has been fertilized, the spiral
cells close, and the upper row of coronula cells is then less crown-like.

The description of N. inaequalis J. Groves (1928, p. 127) bears
some resemblance to that of N. madagascariensis. The outstanding fea-
tures of the former species are: the dactyls partly one, partly two-
celled; frequently occurring clusters of one-celled dactyls at the second
and third branchlet nodes; conspicuously contracted base of the ultimate
cell. None of these characters are to be found in the present species,
in which, moreover, the dimensions of both antheridia and oogonia are
smaller. The following characteristics are common to both species: the
unequal length and complexity of the rays, which, however, in mada-
gascariensis are never curved at their base, and the marked elongation
of the spiral cells of the oogonium.

Through the kindness of the director of the Kew Herbarium
I had the opportunity to study the only specimen of N. inaequalis
extant there. The species may indeed be immediately distinguished by
the remarkable superior cell of the dactyls which is contracted at the
base, and less broad than the inferior cell. The hyaline part of the
cell-wall of the upper cell in N. inaequalis has the same thickness
everywhere, whereas in N. madagascariensis it is considerably thicker
towards the apex than in other parts. These considerations made me
conclude to keep the Lam & Meeruse material separate from N. inaequalis, and to describe it as a new species, also on account of the differences with other allied species to be mentioned underneath.

In the bi to three-celled group N. madagascariensis is closely allied to N. heteroteles Groves & Stephens of which I studied the type, extant in the Kew Herbarium. This plant has quite another habit, being very slender and probably very large, with elongate rays; its size cannot be stated with certainty as the specimen is badly preserved. Other differences are to be found in all parts of the plant. The primary rays are \( \frac{1}{3} \) the length of the total branchlet, being c. 2 cm long; all other rays are nearly of equal length, and the primary ray is often the shortest one. N. madagascariensis, on the other hand, has a tufted habit, the branchlets being short and compact, and up to 1 cm long. The inferior cell of the dactyls is much shorter than in N. heteroteles where it often reaches a length of 5 mm. The length of the oogonia given by Groves & Stephens (1933, p. 277) as about 500 \( \mu \) long, the coronula exclusive, seems to be a little too high: I found the oogonia but very rarely longer than 425 \( \mu \). The ripe oospores are c. 300 \( \mu \) long, i.e. 270—320 \( \mu \), and in by far the most cases less than 300 \( \mu \). The spiral cells never show the lengthening, so remarkable for the new species, and the number of convolutions is always higher, as may be seen in the key below. The different size of the antheridia is also of importance for the determination of the two species.

Though N. madagascariensis shows some similarities with N. micronata (A. Br.) Miq. and varieties, it is at once distinguishable by the size and the shape of the dactyls, by the size and the colour of the gametangia, and by the number of striae. Particularly when the ultimate cell or cells of the dactyls are broken off the inferior cell shows the characteristic truncate, obtusely margined apex.

The taxonomical place and the relationship of N. madagascariensis among the species already known from Madagascar may be expressed in the following key, which at the same time, may serve as a conspectus of the species thusfar known.

**Keys to the Charophyta of Madagascar.**

(Madagascan genera and species are in heavy type).

**Key to the Sections and Genera.**

Cells of coronula in two superimposed series of five cells each; stem and branchlets ecororate; branchlets usually furcate . . . . . . NITELLEAE
Antheridia terminal in the furcations of the branchlets; oogonia lateral; oospore elliptic in transverse section; monoecious or dioecious...

Antheridia and oogonia lateral at the branchlet nodes; oosporer terete in transverse section; sterile branchlets not furcate; fertile branchlets forked with continuous axis; monoecious or dioecious (not yet collected in Madagascar).

Cells of coronula in one series of five cells; stem and branchlets corticate or ecorticate; branchlets never furcate...

Stipulodes absent; bract-cells 1—2 at a node, very long; branchlets consisting of 2—3 very long segments; dioecious, oogonia and antheridia lateral; corticate (not yet collected in Madagascar).

Stipulodes and bract-cells present.

Antheridium situated above the oogonium; corticate (not yet collected in Madagascar).

Lamprothamnium

Antheridium situated at each side of one oogonium; corticate or corticate (not yet collected in Madagascar).

Lychnothamnus

Antheridium situated below the oogonium; monoclista or dioecious; corticate (not yet collected in Madagascar).

Nitellopsis

Chara

Note.

Filarey (1937, p. 490) has described another genus from Western Australia, i.e. Charis F. et G. O. Allen, and though Mr Allen's name is included as an author, he did not see the description before it was published. As the description is only based on vegetative parts of a plant mounted on a microscopical slide, nothing can be said regarding the situation of the gametangia which procure important features for the classification of the genera. It is much to be hoped that an emendation of the description shall be given by Mr Allen, without which nothing can be said with certainty as to the systematical place and validity of this genus.

Key to the species of Nitella Ag. 1824.

(emend. Leenh. 1863) 1) 2).

Each whorl of branchlets consisting of a single uniform series.

HOMOEOCLEMAE

Dactyls (= ultimate rays) each consisting of a single cell.

ANARTHRODACTYLAE

Oogonia 1—3 together, sessile; oospore membrane imperfectly reticulate; antheridium solitary, sessile; branchlets once furcate with long acuminate points; secondary rays 2—4.

1. N. acuminata

Dactyls partly one and partly two-celled.

HETERODACTYLAE

Oogonia 1—2 together; spiral cell elongated at the apex; oospore membrane angularly reticulate; antheridium solitary, sessile; branchlets once to thrice furcate; ultimate cell of dactyl conical, contracted at the base; secondary rays 4—5.

2. N. inaequalis

1) All species hitherto found in Madagascar are monoecious.

2) The nomenclature of smaller groups within the genus seems to need revision.

I hope to deal with this matter in a next paper.
Dactyls each consisting of two or more cells. \( \ldots \) \( \textit{Arthrodactylae} \)

Dactyls always two-celled \( \ldots \) \( \textit{Bicellularae} \)

Dactyls not much abbreviated \( (\text{macrodactylous type}) \); oogonia solitary

First free node of branchlets fertile

Young fertile whorls not enveloped in mucus \( (\text{gymnocephalous type}) \)

Branchlets 2—3 times furcate; secondary rays 3—4; penultimate cell of dactyls narrowed into a distinct neck forming with the apical cell a pronounced muero; oospore c. 280 \( \mu \text{m} \) long; oospore membrane irregularly nodose-recticate; antheridium c. 275 \( \mu \text{m} \) in diam. \( \ldots \)

3. \( \textit{N. ogivalis} \)

Branchlets 3—4 times furcate; secondary rays 6—7; penultimate cell of dactyls very thin (less than 25 \( \mu \text{m} \) in diam.), apical cell very long and slender; oospore 200—250 \( \mu \text{m} \) long; oospore membrane finely reticate; antheridium c. 175 \( \mu \text{m} \) in diam. \( \ldots \)

4. \( \textit{N. tenuissima} \) var. callista

Young fertile whorls enveloped in mucus \( (\text{gloeocephalous type}) \)

Oospore membrane angularly coralloid-recticare; branchlets 3—4 times furcate; secondary rays 5—6; antheridium c. 350 \( \mu \text{m} \) in diam.; \( \sigma^\prime \) and \( \Omega \) gametangia not produced at the same node \( \ldots \)

5. \( \textit{N. Blowiana} \)

Oospore membrane interruptedly granulate; branchlets 2—3 times furcate; secondary rays 4—6; antheridium c. 275 \( \mu \text{m} \) in diam.; \( \sigma^\prime \) and \( \Omega \) gametangia not produced at the same node \( \ldots \)

6. \( \textit{N. vermiculata} \)

First free node of branchlets sterile

\( \sigma^\prime \) and \( \Omega \) gametangia never produced at the same node; oospore membrane imperfectly recticate \( (1) \); branchlets 3—4 times furcate; secondary rays 7; oogonium 530 \( \mu \text{m} \) long; oospore with c. 9 inconspicuous striaae \( \ldots \)

7. \( \textit{N. Baronii} \) \)

\( \sigma^\prime \) and \( \Omega \) gametangia at the same node; oospore membrane finely granulate; branchlets 2—4 times furcate; secondary rays 7; oospore with 7—8 prominent striae, 275—400 \( \mu \text{m} \) long \( \ldots \)

8. \( \textit{N. leptodactyla} \) var. megaspora

Dactyls much abbreviated \( (\text{brachydactylous type}) \); oogonia clustered

Upper cells of corona twice or more as long as the lower ones; oogonia clustered, showing 6 prominent striae; branchlets 1—3 times furcate; secondary rays 3—6; oospore membrane reticate \( \ldots \)

9. \( \textit{N. furcata} \)

Dactyls indifferently two and three-celled

Young fertile whorls not enveloped in mucus \( (\text{gymnocephalous type}) \); oospore less than 325 \( \mu \text{m} \) long

Dactyls more than three-celled; antheridium c. 275 \( \mu \text{m} \) in diam.; oogonia solitary

All free nodes fertile; oospore with 8 broadly flanged striae, warm dark brown; membrane finely reticate; branchlets 2—3 times furcate; secondary rays 3—4; penultimate cell of dactyl rounded at the apex \( \ldots \)

10. \( \textit{N. mucronata} \) var. mobilis

1) Cf. footnote 1 on p. 373.
First free node sterile; oospore with 7—8 thin striae, light golden yellow; membrane finely reticulate; branchlets 2—3 times furcate; secondary rays 5—8 (?); penultimate ray of dactyl tapering at the apex.

11. N. graciliformis
Dactyls as much two as three-celled; antheridium more than 340 μ in diam.; oogonia geminate.

All free branchlet nodes fertile; oospore 275—325 μ long with 6 broad striae, bright yellow brown; membrane angularly reticulate; antheridium frequently not at the first free node, c. 340 μ in diam.; branchlets 2—3 times furcate; secondary rays 3—4; penultimate cell of dactyl straight at the apex, variable in length; apical cell conical, not much varying in length, at the base as wide as the penultimate cell.

12. N. madagascariensis
First free branchlet-node sterile; oospore 270—320 μ long with 8 flanged striae, dark brown; membrane finely and regularly reticulate; antheridium not at the third free node, c. 375 μ in diam.; branchlets 2—3 times furcate; secondary rays 4; penultimate cell of dactyl rounded at the apex; apical cell extremely variable in size, conical.

13. N. heteroteles
Young fertile whorls enveloped in mucus (gloeoccephalous type); oospore 325—400 μ long, membrane angularly reticulate; dactyls mostly three-celled, a few two-celled; branchlets 2—3 times furcate; secondary rays 4—5; upper two nodes sterile; oogonia 1—3 together, "frequently geminate".

14. N. sphaerocephala
Dactyls each consisting of three to six cells (not yet collected in Madagascar).

Each whorl of branchlets consisting of 3 series, viz. one central longer and more compound row in the middle, and two accessory rows, one above and one below the middle-row (not yet collected in Madagascar).

**Key to the species of Chara L. 1754**

Stipulodes in a single whorl.

1) All species hitherto found in Madagascar are monoecious.
2) Cf. note 2 on page 378.
J. S. Zaneveld: *Nitella madagascariensis*, nov. spec., with notes

Rows of cortical cells of stem thrice as numerous as the branchlets (triplostichous type)

Stem corticate, branchlets corticate except the lowest segment (in *C. hydropitys* the stem cortex is sometimes diplostichous) ... 3. *C. hydropitys*

Stipulodes in a double whorl ... .... DIPLOSTEPHANAE

Rows of cortical cells of stem as numerous as the branchlets (not yet collected in Madagascar) ... .... HAPLOSTICHAE

Rows of cortical cells of stem twice as numerous as the branchlets ... .... DIPLOSTICHAE

Secondary cortical cells more prominent than the primary; spine-cells situated in furrows, solitary; posterior bract-cells rudimentary ... 4. *C. vulgaris*

Rows of cortical cells of stem thrice as numerous as the branchlets ... .... TRIPLOSTICHAE

Lowest segment of branchlets corticate ... .... PHYLLOPODES

Cortical cells on branchlets twice as numerous as the bract-cells; lowest branchlet segment moderately long

Stipulodes and spine-cells rudimentary; antheridia c. 500 μ in diam. ... 5. *C. fragilis*

Stipulodes and spine-cells well developed; antheridia 325–350 μ in diam. ... 6. *C. pseudo-brachypus*

Cortical cells on branchlets thrice as numerous as the bract-cells; lowest branchlet segment very short; stipulodes and spine-cells elongated, acute

7. *C. brachypus*

Lowest segment of branchlets ecorticate ... .... GYMNOPODES

Cortical cells on branchlets thrice as numerous as the bract-cells; stipulodes and spine-cells elongated, acute ... 8. *C. zeylanica*

Geographical distribution.

Concerning the distribution of the Madagascan (and three allied) Charophyta the following table may give a survey.

<table>
<thead>
<tr>
<th>Species</th>
<th>Continents</th>
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<tr>
<td><em>Nitella</em></td>
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<tr>
<td>1. <em>acuminata</em> A. Br. 1849</td>
<td>+</td>
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<tr>
<td>2. <em>inaequalis</em> J. Groves 1928</td>
<td>+</td>
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<tr>
<td>3. <em>ogivalis</em> Groves &amp; Stephens 1933</td>
<td>+</td>
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<tr>
<td>4. <em>tenuissima</em> (Desv.) Kütz. 1843</td>
<td>+</td>
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<tr>
<td>var. <em>callista</em> J. Groves 1928</td>
<td>+</td>
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<td>5. <em>Blowiana</em> J. Groves 1928</td>
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<tr>
<td>6. vermiculata J. Groves 1928</td>
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<td>7. Baronii H. &amp; J. Groves 1887</td>
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<tr>
<td>8. leptodactyla J. Groves 1922 var. megaspora J. Groves 1928</td>
<td>+†</td>
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<tr>
<td>9. furcata Ag. 1824</td>
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<tr>
<td>10. mucronata (A. Br.) MIQUEL 1840 var. mobilis J. Groves 1928</td>
<td>+</td>
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<tr>
<td>11. gluciformis J. Groves 1928</td>
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<tr>
<td>12. madagascariensis ZAN. 1939</td>
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<td>13. heteroteles Groves &amp; Stephens 1933</td>
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<tr>
<td>14. sphaerocephala J. Groves 1928</td>
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</table>

**Chara**

1. Benthamii A. Br. 1868 | +    | +    | +    | distribution doubtful |
2. gymnopitys A. Br. 1852 | +    | +    | +    | +    |
3. hydropitys REICH. 1834 | +    | +    |       | +    |
4. vulgaris L. 1753 | +    | +    | +    | +    | +    |
5. fragilis DESV. 1810 | +    | +    | +    | +    |
6. pseudo-brachypus Groves & Stephens 1926 | +    | +    | +    | +    |
7. brachypus A. Br. 1849 | +    | +    |       | +    |
8. zeylanica Willd. 1803 | +    | +    | +    | +    |

The table and the keys show that Madagascar possesses in total 14 species of Nitella and 8 species of Chara, whereas no representative of the other genera have thusfar been found. The Charophyta have 3 genera which are cosmopolitan, two of which are extant in the island.

Of the genus Chara none of the species is endemic, whereas the genus Nitella has 9 endemics, and moreover, 3 varieties restricted to
this particular area only. To the variety megaspora of *N. leptodactyla*, a species which is only recorded from Ceylon, Groves (1928, p. 132) remarks: "With some doubt I place this series of plants under *N. leptodactyla*. Though showing a considerable range of variation they do not seem to differ in any important point, ..." The differences enumerated thereafter show that the variety megaspora is as much distant from *N. leptodactyla* var. typica as *N. pseudoflabellata* or *N. mucosa* from *N. mucronata*. Therefore it would probably be justified to consider it a separate species, in which case the number of endemic species would be 10.

*N. tenuissima* and *N. mucronata* to which belong the other endemic varieties referred to above, are distributed in four of the five continents, Australia excepted. The two not-endemic *Nitella*-species occur in three continents, viz. *N. acuminata* in Asia, America and Africa, and *N. furcata* in Asia, America and Australia. Possibly the last-named species is more widely distributed, as it may have been overlooked, being cited under different names.

The same wide geographical distribution is also found in the *Chara*-species of Madagascar. *C. vulgaris* and *C. fragilis* are cosmopolitan, *C. gymnopitys* and *C. zeylanica* are widely distributed in the tropics and subtropics, lacking in Europe. *C. hydropitys* has nearly the same area as the preceding species, but is not recorded from Australia. *C. brachypus* is found in several tropical localities of the old-world only, and is not extant in Europe and America, *C. pseudo-brachypus* is only recorded from the type localities, i.e. Natal and Southern-Rhodesia. As to the distribution of *C. Benthamii* I may remark that the opinions differ considerably with regard to the differences of the last-named species towards *C. gymnopitys*, which have probably often been confused; their distribution is therefore more or less doubtful.

**Discussion.**

Surveying the whole I may give some additional remarks.

The present find adds another species to the group, which forms a link between the Bicellulate and Pluricellulate-groups of J. Groves's section *Arthrodaetae* (Groves, 1935). In Madagascar there is only one member of the *Anarthrodaetae*, viz. *N. acuminata*. The Pluricellulate-group — Braun's section *Polycystidetae* (1868, p. 797) — is not represented in Madagascar, whereas to the group of the Bicellulatae, which have the ultimate rays strictly two-celled, belong most of the Madagascan members of the genus *Nitella*, viz. 5 endemic species and 2 varieties (cf. key). The other species are to be classified in such a way
that the number of cells composing the ultimate rays (dactyls) gradually increases. Starting with *N. mucronata* var. *mobilis* and *N. graciliformis* which have the dactyls frequently two and rarely three-celled, there are two species with as many two as three-celled dactyls, viz. *N. madagascariensis* and *N. heteroteles*, whereas finally in *N. sphaerocephala* the three-celled dactyls seem to represent the normal condition, as from the 112 dactyls examined by Gaovès (1928, p. 131) 98 were three-celled, and only 14 two-celled. As has already been stated, species with more than three-celled dactyls do not occur in Madagascar, and though they are widely distributed in four continents, monoecious species are not yet recorded from Asia.

In connection with the foregoing some more particulars may be added. Whereas the Madagascarian Bicellulatae are invariably one to four times furcate, the number of furcations in the group with two and three-celled dactyls is always two to three. The number of secondary rays in the latter group is usually 3 or 4, and in the Bicellulatae the variation is much greater, viz. between 3 and 7. *N. graciliformis* of the bi to three-celled group forming an exception as it has 5—8 secondary rays, but on the plate (Gaovès 1928, pl. 4) this number seems to be 3 to 4 (hence the interrogation-mark in our key).

I would further point out that in the two and three-celled group all species, except *N. mucronata* var. *mobilis* ("as far as observed", Gaovès 1928, p. 127) and *N. graciliformis* the oogonia are geminate, whereas all Bicellulate species have solitary oogonia (except *N. furcata*). In the last-named group the membrane of the oospore is granulate or reticulate, in the former it is always reticulate. As has been stated already above no members of the Pluricellulatae have been found in Madagascar nor representatives of the section Heteroclemae to which the cosmopolitan *N. hyalina* Ag. belongs.

As to the genus *Chara* some of the larger groups are entirely lacking in Madagascar, viz. the Haplostephanæae — Ecorticateae, and the Diplostephanæae — Haplostichæae. To the former group belongs *C. Braunii* GMEL., a species occurring all over the world, whereas the latter group has no representatives in Australia.

No endemic *Chara*-species has been recorded from Madagascar. None of the other genera *Tolypella, Nitellopsis, Lamprothamnium and Lychnothamnus*, of which only the first-named is cosmopolitan, are represented in the island.

It is shown in the foregoing that several of the principal sections
of the Charophyta are entirely lacking, but that the groups represented in the island have, in general, a good number of species. This and the other particulars dealt with do not throw any new light on the flora of Madagascar, but merely confirms what was already known: an early isolation and a high antiquity of the island. How the immigration of the Charophyta into Madagascar possibly has taken place may be briefly stated here. As the Charophyta usually grow in rather shallow water, ranging from a few inches to a few feet deep, the distribution by means of running waters cannot be an important one, and the dispersal must be due mainly to the transport of the minute oospores by migratory water-fowl. According to RIDLEY (1930, p. 535) the distribution by means of larger animals drinking at the pools is of importance, as the oospores, little fragments of the plants or bulbils adhering to the body or feet may thus be carried to other places. The Charophyta are very fragile, and fragments of the plants grow readily, staying alive out of water for a considerable time. So I got once specimens of Chara vulgaris and Tolypella nidifica collected more than 14 days before in Corsica and transported in a cover of paper still showing the cyclosis (protoplasmic circulation). On re-immersing the specimens in water they quite recovered. Thus the dispersal by means of adhering to birds or mammals is very well possible. I do not know whether the oospores when eaten, are to be found in the excreta and are still germinative.

Madagascar is situated some 240 miles (= c. 540 km) off the East African coast, a distance which most probably can be covered by migratory birds, especially ducks, geese, etc. At any rate, however, I do not think that Madagascar has got and still gets in this way its Charophyta-flora as the number of African species would then probably be considerably higher. This suggests that the penetration of Charophyta has probably taken place in early times by means of a land connection. According to BAKER (1881) and to BARON (1890, p. 290) Madagascar was connected with the African continent, and also with Mauritius, Bourbon and the Seychelles during some part or parts or the whole of the Miocene (including the Oligocene) and the early Pliocene periods. Moreover, PERRIER DE LA BATHE (1936, p. 142) assumes a connection with Australia in the Upper Cretaceous.

Fossil Charophyta have already been recorded from the Palaeozoic era. Potonie (1901, p. 25) figures a problematic Nitella-like organism from the Silurian, and GROVES and BULLOCK WEBSTER (1924, p. 85) mention one find of the longitudinally flattened fruit of Nitella from a deposit near Moscow, considered interglacial. Other fossil remains of
the genus *Nitella* are of very recent geological dates, probably on account of the fact that the fruits of *Nitella* do not develop a lime shell. Remains of *Chara*-species, however, have been recognized with certainty from the Lower Oolites of the Mesozoic. The first *Tolypella* was found in the Lower Headon Beds (Eocene) of Hordle Cliffs, and *Nitellopsis*-species only in the Pliocene (Cromer Forest Bed) (cf. Groves and Bullock Webster, 1924, pp. 83 and 84). No fossil representatives of the genera *Lamprothamnium* and *Lychnothamnus* have been collected as yet.

On account of the existence of fossil Charophyta of very early geological periods, I think it most plausible that the intrusion of Charophyta into Madagascar took place along the way of an isthmus. Only very few species have thus reached Madagascar, and whereas some of them may have arrived at the cost of some loss of their potentialities (Lam, 1938), others have apparently come to a rich display of forms possibly by activated latent genes 1). This fully agrees with what has been found in the Madagascarian Charophyta where in some of the sections the characters vary very much, and in other ones they seem to have come to a standstill. In this sense I agree with Braun's expression (1868, p. 790): "Ein spezifischer Typus kann in Wirklichkeit entweder durch eine einzige Art, oder auch durch mehrere Arten repräsentirt sein".

**Literature cited.**


1) In a subsequent paper on the Malaysian Charophyta to be published in this journal, I hope to refer again to this subject.
J. S. Zaneveld: Nitella madagascariensis, nov. spec., with notes


