Vegetative and reproductive morphology of *Ganonema lubrica* sp. nov. (Liagoraceae, Rhodophyta) from the Canary Islands

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The marine red alga *Ganonema lubrica* sp. nov. (Liagoraceae, Nemaliales) from the Canary Islands is described. Gametophytes are terete, lubricous, lightly calcified, and radial to irregularly paniculately branched. Axes consist of many (18–26) primary medullary filaments that give rise to cortical fascicles with subcylindrical or clavate basal cells. Spermatangia form dense clusters on subterminal cortical cells, displacing the terminal cell laterally. Carpogonial branches are straight, five to eight cells in length, and arise from inner cortical supporting cells in positions occupied by adventitious cortical filaments. The carpogonium divides transversely and the upper half gives rise to a compact subhemispherical carposporophyte. Sterile filaments are absent or arise from the suprasupporting cell and partially or completely surround the carpogonial branch. Gonimoblastic rhizoids sometimes are present. *Ganonema lubrica* differs from previously described species of *Ganonema* and of the Mucosae group of *Liagora* mainly in the architecture of carpogonial branches, the shape of the basal cell of cortical fascicles, the derivation of most sterile filaments from the suprasupporting cell, and the occasional production of rhizoids from the gonimoblast.

INTRODUCTION

The red algal genus *Ganonema* was erected by Fan & Wang (1974) based on *Liagora farinosa* Lamouroux, and later it was rejected by Abbott (1984) in favor of a broader definition of *Liagora* Lamouroux. Kraft (1989) showed that, among the genera of Liagoraceae, *Liagora* has been too broadly defined, and recently Huisman & Kraft (1994) proposed the reinstatement of an emended genus *Ganonema* for plants with the following combination of characters: (1) calcification heavy to absent; (2) branches multiaxial with longitudinal medullary filaments bearing lateral cortical fascicles on swollen, highly differentiated basal cells; (3) adventitious rhizoids bearing subsidiary cortical fascicles common; (4) cells of mature medullary filaments broad (>40 μm in diameter); (5) carpogonial branches straight or slightly curved, occupying positions of vegetative cortical laterals on primary filaments and also on subsidiary cortical and rhizoidal filaments, frequently compound; (6) carposporophyte compact, with terminal carposporangia and little or no postfertilization fusion of carpogonial branch cells; and (7) spermatangia in dense, dendroid clusters. According to Huisman & Kraft (1994), these features are displayed by *Ganonema farinosa* (Lamouroux) Fan et Wang and related species and, apparently, by many of the present members of the Mucosae group of the genus *Liagora*.

The section Mucosae of *Liagora* was established by Yamada (1938) to include very soft and lubricous, slightly calcified plants possessing straight carpogonial branches located in positions like those of vegetative cortical filaments. The remaining species of *Liagora* are characterized by more calcification and curved carpogonial branches borne laterally on cortical cells (Kraft 1989). According to Yamada (1938), four species were initially recognized in the Mucosae: *Liagora*

dendroidea (P. et H. Crouan in Mazè et Schramm) Abbott (as *L. mucosa* Howe, the type species of the section), *L. mucosissima* Yamada, *L. orientalis* J. Agardh (as *L. formosana* Yamada) and *L. pedicellata* Howe. Later, the new species *L. samaensis* Tseng (Tseng 1941) and *L. amplectens* Abbott (Abbott 1984) were added, and others (*L. mucosissima* and *L. pedicellata*) were transferred by Abbott & Doty (1960) to the genus *Trichogloeopsis* Abbott et Doty. Finally, Abbott (1990a) included *Liagora pectinata* Collins et Harvey in this group, establishing some synonyms and emphasizing the useful features for delineating some mucosoid taxa. Species of the Mucosae group have not been reinvestigated yet in the light of the taxonomic criteria proposed by Huisman & Kraft (1994). Thus only three species of *Ganonema* are currently recognized: *G. farinosa*, widespread in warm temperate and tropical seas throughout the world (Abbott 1990b, Kvaternik *et al.* 1996), *G. codii* (Womersley) Huisman et Kraft from South Australia and Victoria (Huisman & Kraft 1994, Womersley 1994), and *G. helminthaxis* Huisman et Kraft from Western Australia (Huisman & Kraft 1994). A fourth species, *G. pinnatiramosa* (Yamada) Fan et Wang (Fan & Wang 1974) from Japan, has been considered a forma of *G. farinosa* (Abbott 1984, 1990b).

During recent taxonomic studies carried out on the Liagoraceae of the Canary Islands (Kvaternik & Afonso-Carrillo 1995; Kvaternik *et al.* 1996), abundant specimens of a highly lubricous liagoroid alga were examined. Previously, in some specimens of these plants, Audiffred (1985) and Gil-Rodríguez *et al.* (1985) observed rhizoids arising from the gonimoblasts, a feature considered to occur exclusively in *Trichogloeopsis* (Abbott & Doty 1960). New observations carried out on numerous, largely fertile specimens showed obvious differences from *Trichogloeopsis pedicellata* (Howe) Abbott et Doty and have allowed us to verify sparse, inconsistent occurrence of gonimoblastic rhizoids. These Canary

Islands specimens showed a combination of attributes that seems exclusive to the genus *Ganonema,* but they differ from previously described species of the *Ganonema*-Mucosae group complex in several features, including the architecture of carpogonial branches, shape of the basal cell of cortical fascicles, derivation of most sterile filaments from the suprasupporting cell, and occasional production of rhizoids from the gonimoblasts. Therefore, a new species is described in this paper based on these specimens.

MATERIALS AND METHODS

Liquid-preserved specimens were fixed in 4% formalin in seawater. Selected fragments were decalcified in 1–5% HCl, washed in seawater, stained in 1% aqueous aniline blue, mounted in a 50% Karo® corn syrup solution, and squashed slightly to separate the filaments. Dried specimens from herbaria were rehydrated in 4% formalin in seawater before decalcification. Micrographs were taken on a Zeiss microscope and drawings were made using a camera lucida. Herbarium abbreviations follow Holmgren *et al.* (1990). Cell measurements are given as diameter × length.

OBSERVATIONS AND DISCUSSION

Ganonema lubrica Afonso-Carrillo, Sansón et Reyes, sp. nov.

Figs 1–37

DIAGNOSIS: Plantae saxicolae, erectae usque 22 cm altae, axes lubrici, leviter calcificati circum medullam, cylindrici usque 3 mm diametro, radiatim versus irregulariter paniculatim ramificati. Rami multiaxiales, medulla multis (18–26) filamentis medullosis primariis et numerosis rhizoideis, cortex fasciculis assimilantibus cellulis ellipsoideis usque moniliformibus, portatis cellulis basalibus subcylindricis vel clavatis. Plantae dioicae. Spermatangia formantia densos racemos super cellulis corticalibus subterminalibus separantibus lateraliter cellulam terminalem. Rami carpogoniales (5–)6(–8) cellulis, orti 1(–2) super cellulis internis sustinentibus, in loco occupato filamentis corticalibus adventiciis. Postfecundationem carpogonium dividens transversaliter et medianum superius oritur compactum subhemisfericum gonimoblastum, usque 250 μm diametro, carposporangiis terminalibus. Carposporangia obovoidea, 10–18 μm × 15–25 μm. Sine conjunctione cellulari. Filamenta sterilia communia orientia cellulis supra sustinentibus et circumdantibus partim aut omnino ramum carpogonialem sed non carposporophytum maturum. Rhizoidea gonimoblastica rara et inconspicua. Tetrasporangia ignota.

Plants saxicolous, erect, to 22 cm in height, the axes lubricous, lightly calcified around the medulla, terete, to 3 mm in diameter, radially to irregularly paniculately branched. Branches multiaxial, the medulla consisting of many (18–26) primary medullary filaments and numerous rhizoids, the cortex consisting of fascicles of ellipsoid to moniliform assimilatory cells arising from subcylindrical or clavate basal cells. Plants dioecious. Spermatangia forming dense clusters on subterminal cortical cells displacing the terminal cell laterally. Carpogonial branches (5–)6(–8)-celled, borne 1(–2) on inner cortical supporting cells in positions occupied by adventitious cortical filaments. Following fertilization the carpogonium divides transversely and the upper half gives rise to a compact subhemispherical gonimoblast, to 250 μm in diameter, with terminal, obovoid carposporangia, 10–18 μm × 15–25 μm. Fusion cell lacking. Sterile filaments common, arising from suprasupporting cell and surrounding, partially or completely, the carpogonial branch, but not the mature carposporophyte. Gonimoblastic rhizoids rare and inconspicuous. Tetrasporangia unknown.

HOLOTYPE: TFC Phyc. 8504 (Fig. 1). Female gametophyte; 4–6 m depth, Roque de Bonanza, El Hierro, Canary Islands, 22 April 1993; leg. *J. Afonso-Carrillo & B. Rojas.*

ETYMOLOGY: The specific epithet refers to the extremely slippery habit.

DISTRIBUTION: Canary Islands (El Hierro, La Palma, Tenerife and Gran Canaria).

REPRESENTATIVE SPECIMENS EXAMINED: EL HIERRO: Roque de Bonanza (*J. Reyes & M. Sansón,* 9 February 1990, 4–6 m depth, female: TFC Phyc. 9873, 9874, 9878; male: TFC Phyc. 8831, 9879), (*J. Afonso-Carrillo & B. Rojas,* 22 March 1992, 4–6 m depth, female: TFC Phyc. 8520, 8522, 8523, 8832; male: TFC Phyc. 9872, 9876). La Caleta (*J. Afonso-Carrillo,* 1 May 1979, 3 m depth, female: TFC Phyc. 2221). La Restinga (*J. Afonso-Carrillo & B. Rojas,* 21 March 1992, tide pool, female: TFC Phyc. 8479, 8513, 8519; male: TFC Phyc. 8514, 8518). Pozo de Las Calcosas (*J. Afonso-Carrillo & B. Rojas,* 16 June 1992, 3–4 m depth, female: TFC Phyc. 8500, 8517, 8521, 9871). LA PALMA: Punta Malpique (*Cancap,* 28 May 1980, 4–10 m depth, female: TFC Phyc. 4305). Teneguía (*M.C. Gil-Rodríguez, J. Afonso-Carrillo, R. Haroun & M. Izquierdo,* 14 June 1983, 5 m depth, female: TFC Phyc. 3122). TENERIFE: Icod (*M.C. Gil-Rodríguez,* 2 August 1976, female: TFC Phyc. 1802). Agua Dulce (*E. Ballesteros, J. Romero & J. Reyes,* 16 July 1993, 10 m depth, female: TFC Phyc. 8516). Las Eras (*E. Guadalupe,* 26 July 1993, 3–4 m depth, female: TFC Phyc. 8515). Bajamar (*I. Ocejo,* 15 April 1997, 4–6 m depth, female: TFC Phyc. 9877). GRAN CANARIA: Las Canteras (*D. Kvaternik,* 11 July 1993, 4 m depth, female: TFC Phyc. 8488).

HABITAT AND SEASONALITY: *Ganonema lubrica* grows on cobble and bare rocks at depths ranging from 3 to 10 m, although occasionally it was collected in low tide pools. It is an early spring–summer annual, and usually is found in areas of moderate water movement. In some areas during these months, *G. lubrica* is a dominant element of the flora, together with other red algae, such as *Acrosymphyton purpuriferum* (J. Agardh) Sjöstedt, *Thuretella schousboei* (Thuret) Schmitz, and several species of *Liagora.* Differences in seasonality occur among populations of the different islands of the Canaries. At El Hierro, the most southwestern island of the Canaries, plants were well developed, reproductive, and abundant from early February (midwinter) to June (late spring), after which they were senescent or absent. Around the other islands, this species appears to be a strict spring–summer annual.

HABIT: Plants are erect, arising from a single small discoid holdfast, to 22 cm in height, mucilaginous, lubricous, and radially to irregularly paniculately branched (Figs 1, 2). Well-developed plants are whitish rose-red when alive, with all branches terete and lightly calcified around the medulla. Main axes are 1–3 mm in diameter, often with several short lateral branches, 1–2 mm in diameter, arising from all sides of the main axes (Figs 1, 2). Entire plants and individual major axes are pyramidal in outline, although branching in pressed specimens can appear as alternate-distichous or unilateral (Fig. 3).
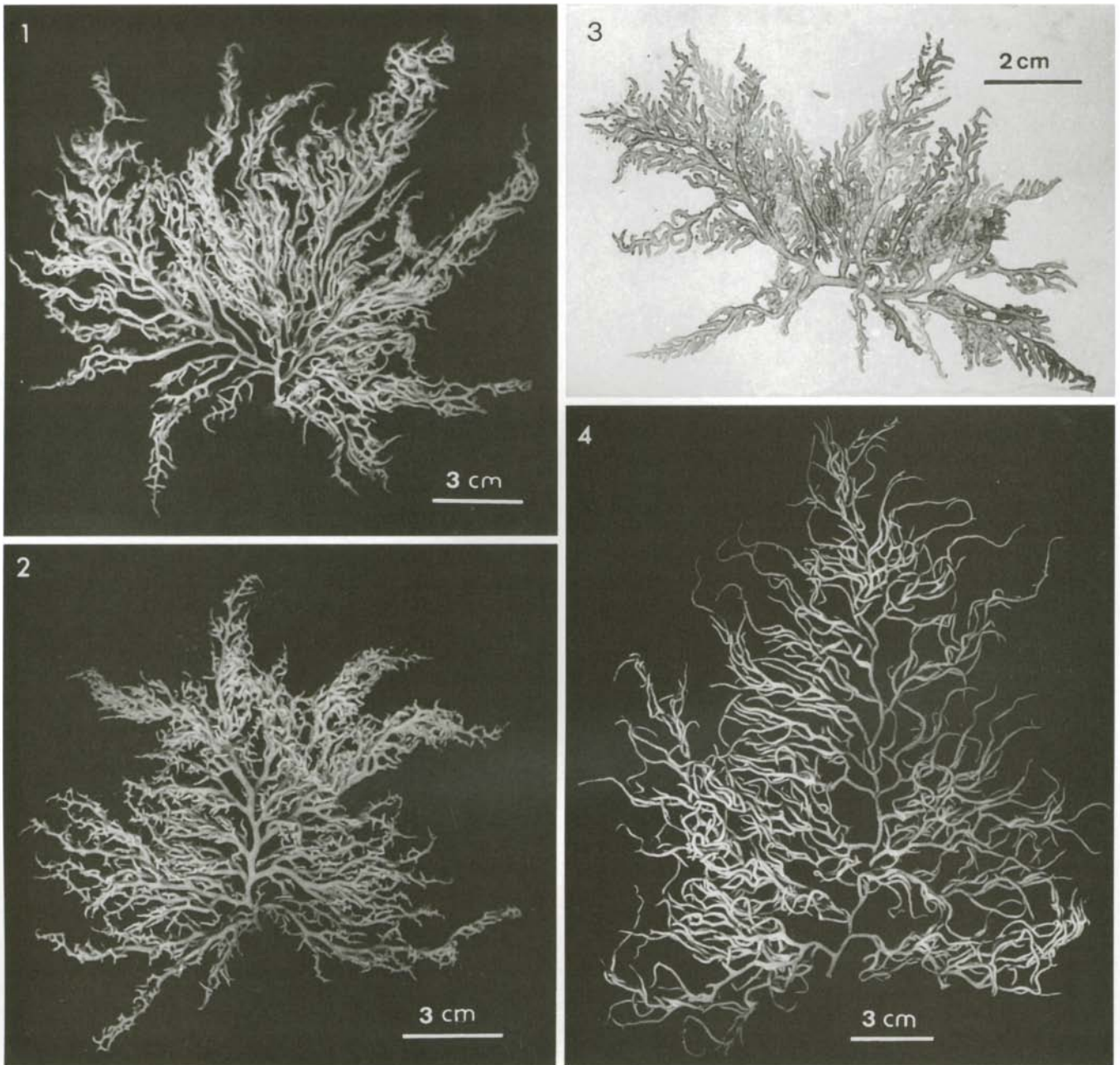
Abbreviations for Figs 1–37. b, basal cell of cortical fascicle; c.f, adventitious cortical filament; g.rh, gonimoblastic rhizoids; h, hair; m.f, medullary filament; rh, rhizoid; s, supporting cell; st.f, sterile filament.

Figs 1–4. *Ganonema lubrica* sp. nov.
  Fig. 1. Liquid-preserved holotype (TFC Phyc. 8504).
  Fig. 2. Liquid-preserved male gametophyte showing the pyramidal outline of the major axes (TFC Phyc. 8831).
 **Fig. 3.** Pressed male gametophyte (TFC Phyc. 9879).
  Fig. 4. Liquid-preserved senescent female gametophyte showing irregularly elongated lateral branches (TFC Phyc. 8516).

Senescent (but fertile) plants become more calcified, brown-yellowish in color, and irregular elongation of the lateral branches leads to the loss of the pyramidal appearance of the thallus (Fig. 4).

VEGETATIVE STRUCTURE: Axes are multiaxial (Figs 5, 6), with a conspicuous central medulla composed of 18–26 filaments, with cells ranging from 5–10 μm × 20–200 μm at the apical 2 mm of axes to 150 μm × 1700 μm at 3 cm from the apex. Each cell of each medullary filament branches distally to form

a cortical fascicle oriented outward at right angles to the medullary axis (Fig. 6). The medulla becomes surrounded by numerous colorless, branched rhizoids (5–12 μm in diameter) that arise from the basal one to three cells of cortical fascicles.

Cortical filaments are 7- to 10-celled, up to 450 μm in length, and are four or five times pseudodichotomously to trichotomously branched (Figs 7, 8). Much of the branching arises from adventitious initials that develop distally on cells of the filaments (Fig. 7). The basal cell of cortical fascicles is
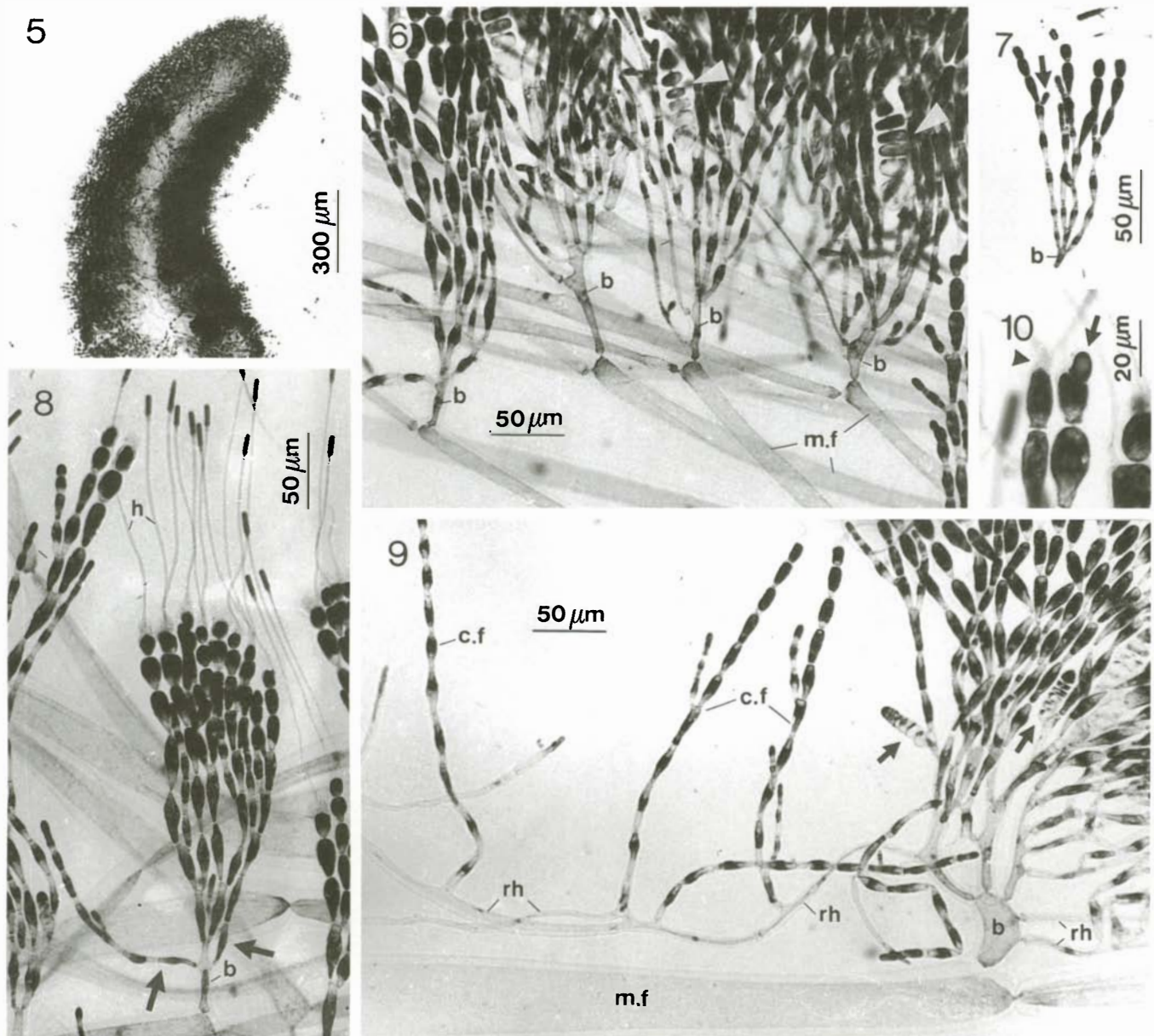
Figs 5–10. *Ganonema lubrica* sp. nov. (Holotype TFC Phyc. 8504 unless stated).
Fig. 5. Branch apex (TFC Phyc. 8523).
Fig. 6. Surface view of an axis showing the origin of cortical fascicles from medullary filaments and carpogonial branches (arrowheads) from cortical cells.
Fig. 7. Detail of a little-developed cortical fascicle obtained from the apex branch showing the initiation of an adventitious cortical filament (arrow).
**Fig. 8.** Cortical fascicle showing adventitious cortical filaments arising laterally from the basal cell of the cortical fascicle (arrows) and numerous terminal hairs.
Fig. 9. Well-developed cortical fascicle showing young carpogonial branches (arrows). Note the origin of rhizoids from the basal cell of the cortical fascicle from which individual cortical filaments arise perpendicularly.
Fig. 10. Detail of terminal cells of cortical filaments, showing a presumed gland cell (arrow) and remnant cell walls (arrowhead).

initially subcylindrical and similar in size and shape to the remaining inner cortical cells (Figs 7, 8), later becoming swollen to irregularly clavate, up to 24 μm × 100 μm in mature fascicles (Fig. 9). Adventitious cortical filaments and rhizoids are common, arising from the basal cell (Fig. 9). Rhizoids produce perpendicularly adventitious cortical filaments and cortical fascicles, and occasionally they grow into the cortex and produce terminal cells with sizes and shapes of typical cortical cells (Figs 8, 9). The other cells of cortical fascicles are elongate to ellipsoid near the base, becoming shorter and moniliform distally (Fig. 8). The outer cortical cells are ovate (7–16 μm × 19–50 μm) to subspherical (7–12 μm in diameter), showing a conspicuous central pyrenoid. In young axes, terminal cortical cells often bear one or two elongate hairs terminated by a slightly dilated and darkly stained tip (Fig. 8) and sometimes one or two cells, assumed to be gland cells or
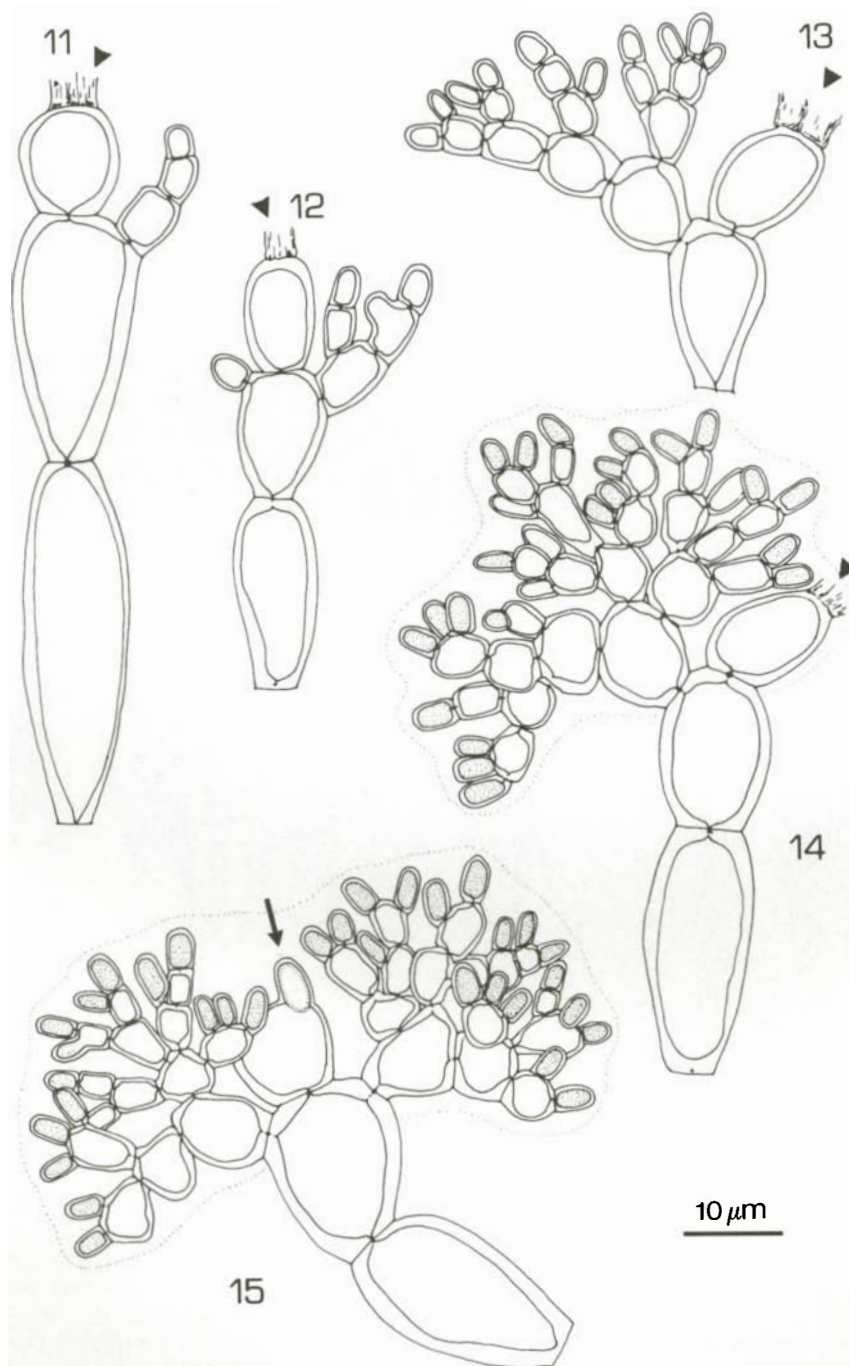
Figs 11–15. *Ganonema lubrica* sp. nov. (TFC Phyc. 8831).
   Figs 11–13. Early developmental stages of spermatangial clusters arising from subterminal cortical cells. Remnant walls (arrowheads) of presumed gland cells are present on the terminal cells.
   **Fig. 14.** Mature spermatangial cluster formed from one spermatangial branch initial with terminal spermatangia.
   Fig. 15. Mature spermatangial clusters produced by two spermatangial branch initials. A presumed gland cell (arrow) is present on the terminal cell. Note spermatangial clusters embedded in a mucilaginous matrix (stippled lines).

remnant cell walls (Fig. 10). Old axes become denuded, persisting as rather compacted medullary and rhizoidal filaments encircled by relatively continuous calcification.

REPRODUCTION: Gametophytes are dioecious. One or two spermatangial branch initials arise on subterminal cells of cortical filaments (Figs 11– 13) and grow to four cells in length, producing lateral branches. Cells of the spermatangial branch are progressively smaller, producing two to six spermatangial mother cells, which in turn cut off two to four ovoid spermatangia 3–4 μm in diameter. The terminal cortical cell bears one, sometimes two, presumed gland cells (Fig. 15) or their remnant cell walls (Figs 11–14), together with mature spermatangial heads embedded in a mucilaginous matrix (Figs 14, 15). Mature spermatangial branches displace the terminal cor-
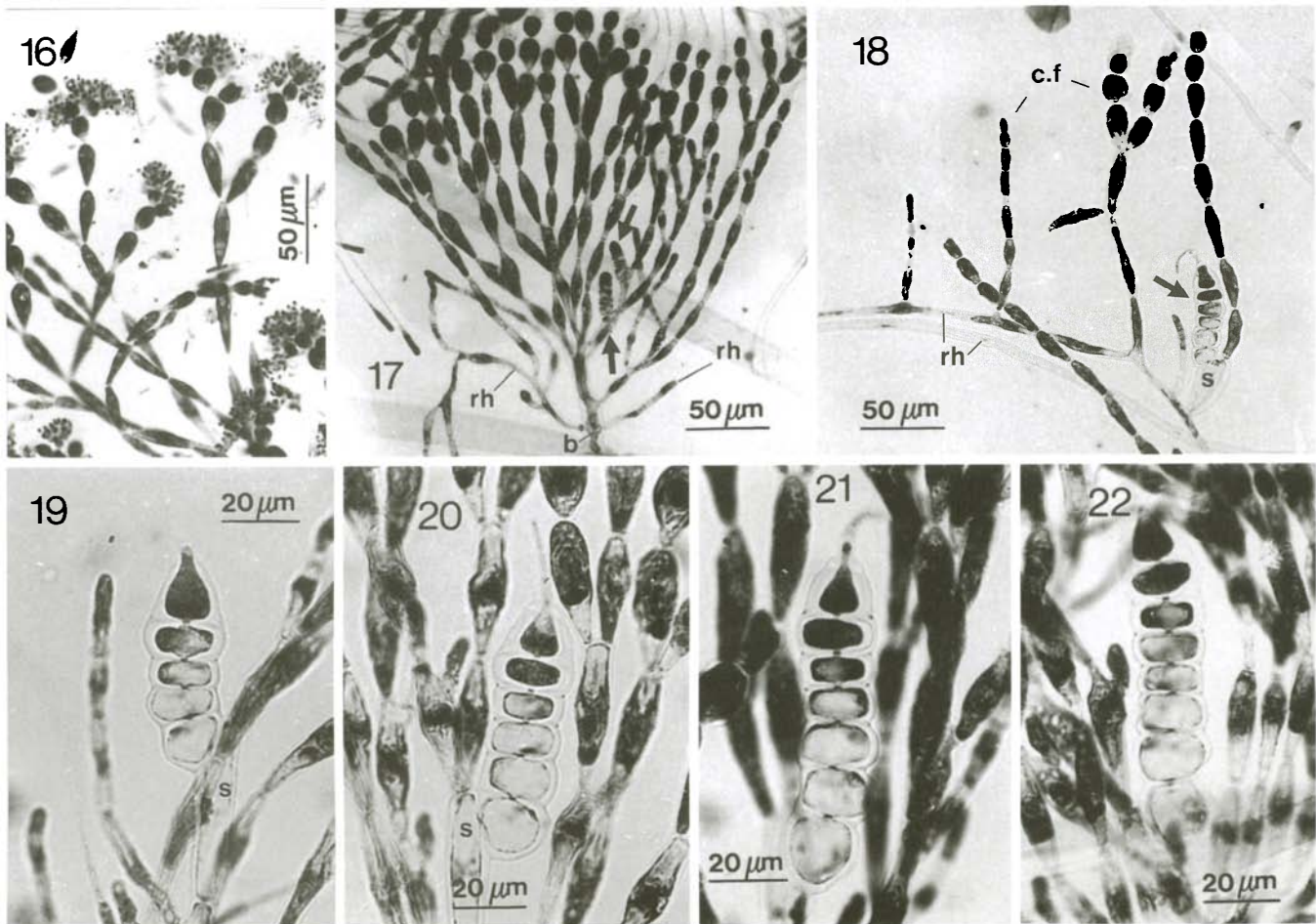
Figs 16–22. *Ganonema lubrica* sp. nov. (Holotype TFC Phyc. 8504 unless stated).
Fig. 16. Cortical filaments bearing spermatangial clusters (TFC Phyc. 8831).
Fig. 17. Young carpogonial branches (arrows) borne on inner cortical cells.
Fig. 18. Carpogonial branch (arrow) borne on the basal cell of an adventitious cortical filament formed from a rhizoid.
Fig. 19. A five-celled carpogonial branch.
Fig. 20. A six-celled carpogonial branch with the corbel-like basal cell arising laterally from the supporting cell. Note the perpendicular orientation of the two pit connections at the carpogonial branch basal cell.
**Fig. 21.** A seven-celled carpogonial branch.
Fig. 22. An eight-celled carpogonial branch. Note that in all carpogonial branches only the carpogonium and one to three hypogynous cells are darkly stained.

tical cell laterally; therefore, spermatangial heads look terminal (Figs 14–16).

Conspicuous carpogonial branches, to 80 μm long, are common in the apical 3 cm of axes and are formed on well-developed cortical filaments. Carpogonial branches arise mostly on the basal two to four cells of cortical fascicles (Fig. 17) but can occur on the basal cell of adventitious cortical filaments formed by rhizoids (Fig. 18). Carpogonial branches are straight and are borne laterally near the distal end of supporting cells in positions otherwise occupied by vegetative cortical filaments (Figs 19, 20). They consist of (5–)6(–8) cells, usually with only the carpogonium and hypogynous cells darkly stained prior to fertilization (Figs 19–22). All cells of carpogonial branches differ from those of typical cortical filaments in being broader than long (12–22 μm × 8–12 μm), except for the larger subhemispherical basal cell and the conical carpogonium (Figs 19–22). The pit connection between the supporting cell and the basal cell of the carpogonial branch is lateral, resulting in a corbel-like basal cell (Fig. 20). The

trichogyne extends beyond the cortex and often has several spermatia attached to it. A single carpogonial branch is normally formed by a supporting cell, but bicarpogonial supporting cells are common in old plants (Figs 23, 24). Rhizoidal filaments were occasionally observed arising from the basal cell of some of these carpogonial branches (Fig. 24), and aborted carpogonial branches sometimes produced a small number of cortical-type cells (Figs 25, 26).

After presumed fertilization, the base of the trichogyne is plugged and the carpogonium extends slightly. The first division of the carpogonium is transverse (Fig. 27), and only the shorter distal part is involved in gonimoblast production (Figs 28–31). Cells of the carpogonial branch become darkly stained, but a fusion cell does not occur (Fig. 31). Mature carposporophytes are subhemispherical (Figs 32, 33), to 250 μm in diameter, and consist of a mass of compact pseudodichotomously and trichotomously branched filaments (Fig. 35), with terminal obovoid carposporangia, 10–18 μm × 15–25 μm. Residual carposporangial walls are retained, suggesting
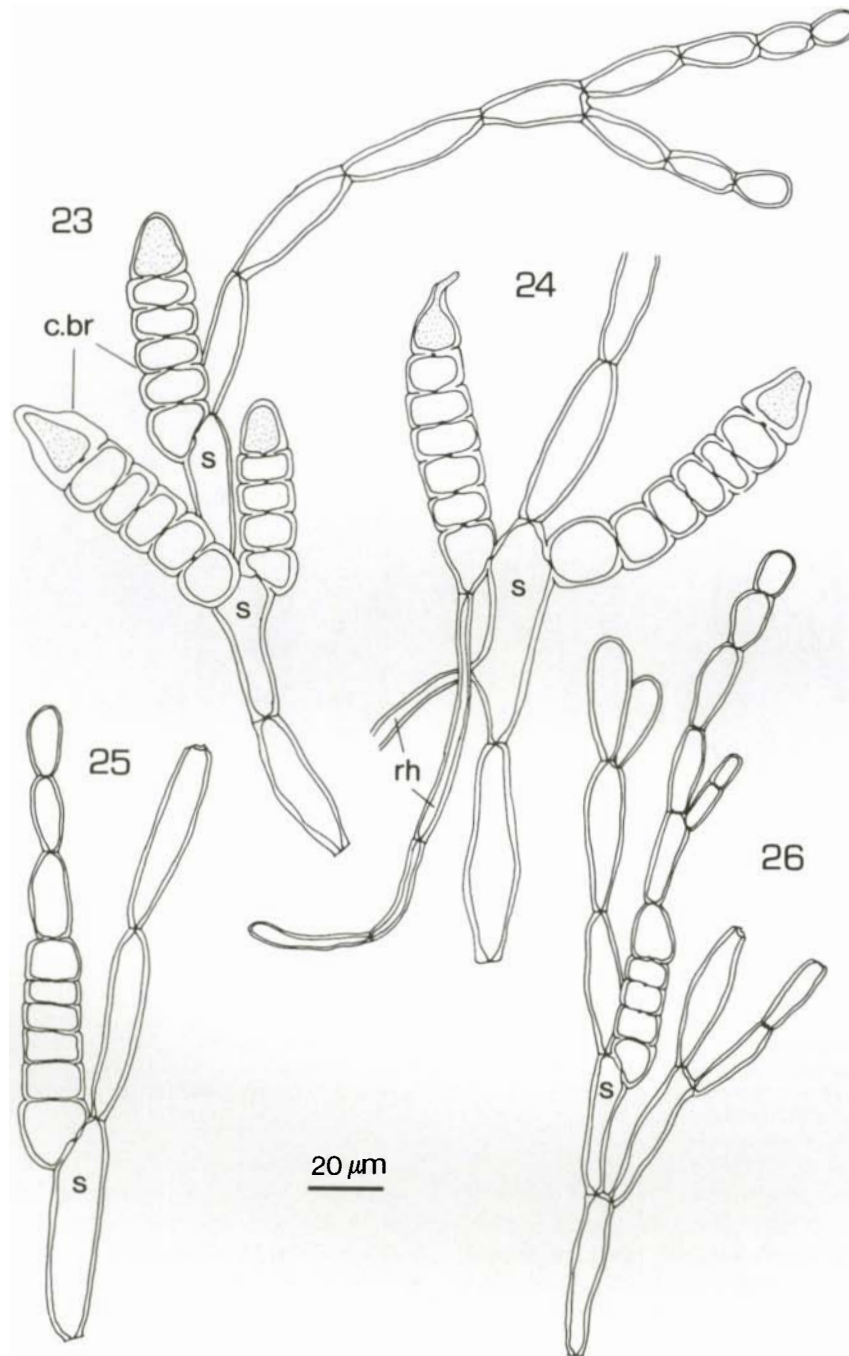
Figs 23–26. *Ganonema lubrica* sp. nov.
   Fig. 23. Two successive supporting cells, the inner bearing two carpogonial branches (TFC Phyc. 8516).
   Fig. 24. Bicarpogonial supporting cell. Note the occurrence of rhizoids from both the basal cell of a carpogonial branch and supporting cell (TFC Phyc. 2516).
   **Fig. 25.** Aborted carpogonial branch forming three cortical-type cells distally (TFC Phyc. 8523).
   Fig. 26. Aborted carpogonial branch forming a branched cortical-type filament distally (TFC Phyc. 8504).

that carposporangial regeneration occurs (Fig. 34). In a few specimens, one to three colorless rhizoidal filaments were produced from lower cells of the gonimoblasts (Fig. 35). These gonimoblastic rhizoids were generally unbranched, thin (5–10 μm in diameter) and short (to 100 μm in length). They grew downward toward the supporting cell beside the carpogonial branch without surrounding it (Fig. 35).

   Simultaneous to gonimoblast development, sterile filaments

are produced from cortical cells adjacent to the carpogonial branch (Figs 36, 37). The development attained by these sterile filaments is highly variable within the same area of the thallus. Sterile filaments can be absent, presenting an entirely naked carpogonial branch below the mature carposporophyte. When sterile filaments occur, they begin to form after gonimoblast initiation (Figs 28, 29) and only occasionally before the first zygote division. Two (rarely three) hyaline, sterile
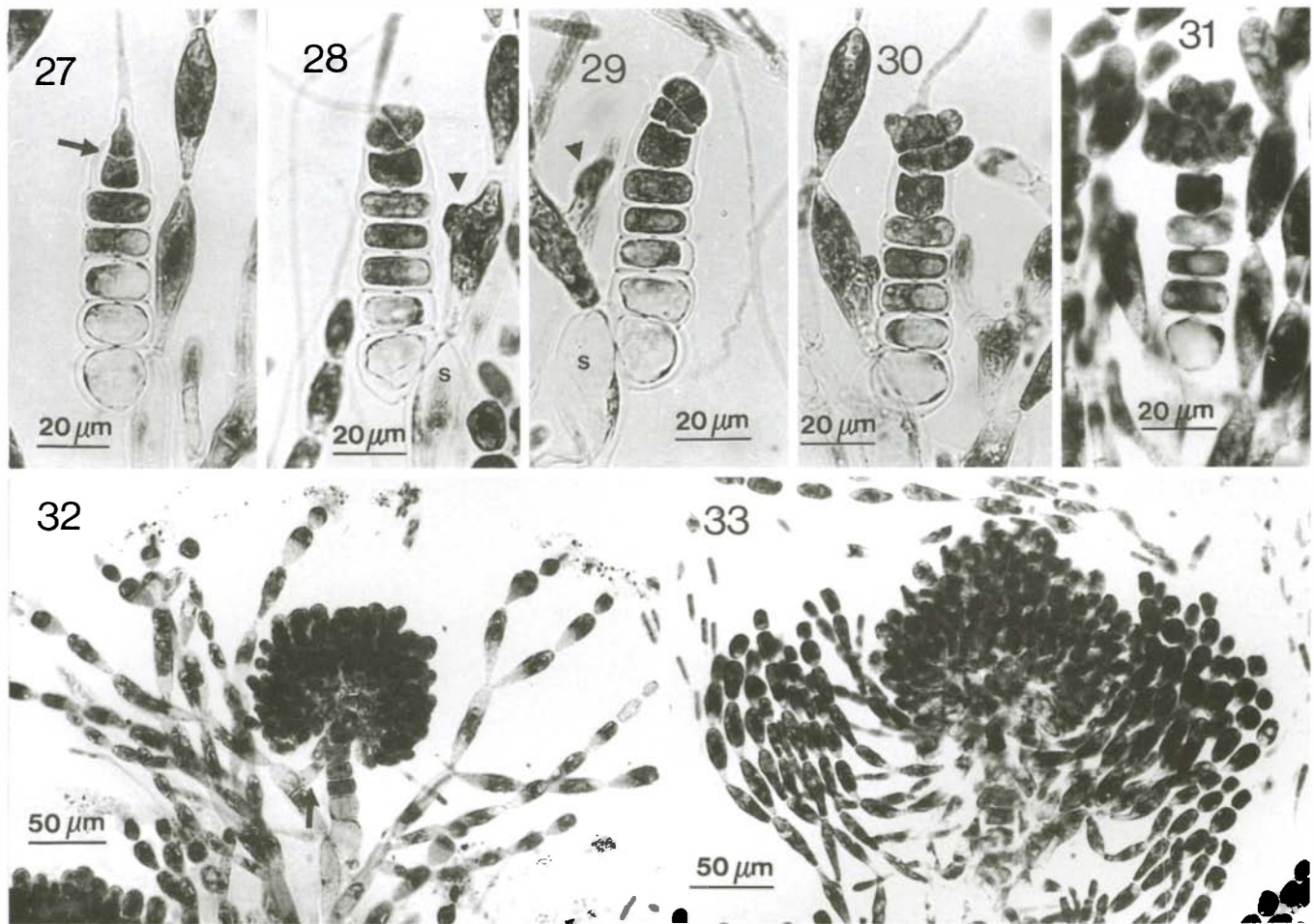
Figs 27–33. *Ganonema lubrica* sp. nov. (Holotype TFC Phyc. 8504 unless stated).
Fig. 27. First transverse division of the carpogonium (arrow).
Figs 28–31. Early development stages of carposporophytes with only the distal half of the carpogonium taking part in gonimoblast production. Sterile filaments (arrowheads) arise from suprasupporting cells toward the carpogonial branch.
Fig. 32. Mature carposporophyte. Short sterile filaments (arrow) grow toward the carpogonial branch (TFC Phyc. 8523).
Fig. 33. Mature carposporophyte with extensive development of sterile filaments around cells of the carpogonial branch, some of them producing cortical-type filaments laterally.

filaments arise laterally and opposite from the suprasupporting cell, curving and growing toward the carpogonial branch, eventually embracing it (Figs 32, 36). The development of these sterile filaments may be scanty and limited to a few cells that partially encircle a portion of the carpogonial branch in mature carposporophytes (Fig. 36), or the sterile filaments may be long and branching, and curl around all the cells of the carpogonial branch, without surrounding or intermingling with the gonimoblasts (Fig. 37). Cells of these sterile filaments sometimes become inflated and produce laterally uniseriate pigmented filaments of cortical-type cells (Figs 33, 37).

REMARKS: Observations on *Ganonema lubrica* from the Canary Islands clearly show that this species is a member of the Liagoraceae. Plants are lubricous and multiaxial, and gonimoblasts arise directly from the carpogonium. Nevertheless, its generic placement needs additional comment. *Ganonema lubrica* appears to display all significant attributes used by Huisman & Kraft (1994) to delineate the genus *Ganonema*, except its unexpected gonimoblastic rhizoids. This and some other characters will be discussed below.

The occurrence of rhizoids produced by the gonimoblasts

seems to be the most controversial character observed in *Ganonema lubrica*. The production of gonimoblastic rhizoids (gonimorhizoids) is currently accepted as an exclusive feature of the genus *Trichogloeopsis* (Abbott & Doty 1960; Kraft 1989). Other important characters defining *Trichogloeopsis* are the presence of naked carposporophytes, owing to the absence of sterile postfertilization filaments, and the particular architecture of carpogonial branches that occurs frequently in the terminal few cells of a cortical filament (Kraft 1989). Both features are absent in *Ganonema lubrica*. In the new species, sterile filaments occurred close to the carpogonial branch below the carposporophyte, although naked carposporophytes were occasionally observed. Carpogonial branches, with all cells differing from typical cortical filaments, always occurred toward the distal ends of supporting cells, but were never terminal on a cortical filament. On the other hand, the gonimorhizoids observed in *Ganonema lubrica* occurred sparsely in a few of the specimens, and they were inconspicuous filaments that never reached the extensive development described for those species included by Abbott & Doty (1960) in the genus *Trichogloeopsis*. A proposal to extend the definition of
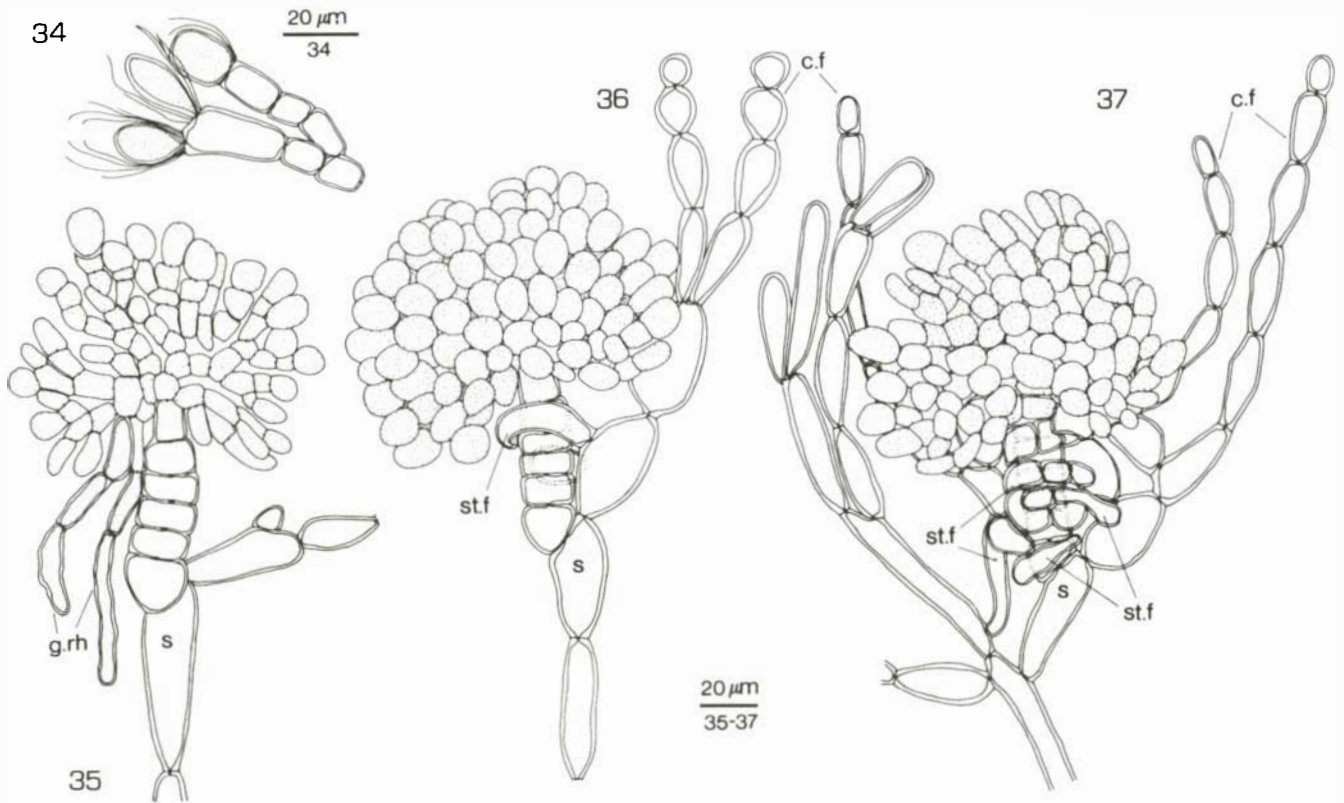
Figs 34–37. *Ganonema lubrica* sp. nov.
Fig. 34. A fragment of a mature gonimoblast showing three carposporangia and residual carposporangial walls (TFC Phyc. 8517).
Fig. 35. Mature carposporophyte showing the pseudodichotomously and trichotomously divided filaments and two gonimoblastic rhizoids (TFC Phyc. 8523).
Fig. 36. Mature carposporophyte showing the carpogonial branch partially surrounded by two sterile filaments arising from the suprasupporting cell (TFC Phyc. 8523).
Fig. 37. Mature carposporophyte showing sterile filaments curling around all cells of the carpogonial branch. Note the production of filaments of cortical-type cells from cells of sterile filaments (TFC Phyc. 8522).

Trichogloeopsis to include the new species would be incongruent because of the inconsistent occurrence of both the naked carposporophytes and gonimorhizoids exhibited by *Ganonema lubrica*.

Ganonema lubrica exhibits a medulla formed by coarse filaments, up to 150 μm in diameter, and cortical fascicles arising from basal cells slightly longer and more swollen than the remaining inner cortical cells. The basal cell of cortical fascicles seems to play an important role in the structure of the axis, as described by Huisman & Kraft (1994) in *G. helminthaxis*. In both species, primary cortical filaments and additional adventitious filaments arise from the distal end of the basal cell, whereas adventitious cortical filaments and rhizoids arise laterally. These rhizoids continue their horizontal growth and produce a large number of perpendicular cortical filaments. In *Ganonema farinosa* (Kvaternik *et al.* 1996), *G. helminthaxis* (Huisman & Kraft 1994), *G. codii* (Womersley 1965, 1994, as *Liagora codii*), and apparently in some species of the section Mucosae, e.g. *Liagora dendroidea* (Desikachary & Balakrishnan 1957, as *L. mucosa*), the cortical fascicles arise from a short, broad basal cell, which is different from *Ganonema lubrica*. But probably, the shape of these basal cells is not a feature exclusive to *G. lubrica*. At least one species of the Mucosae group, *Liagora samaensis,* has been

described as possessing a subcylindrical or clavate cell at the base of cortical fascicles (Tseng 1941).

Ganonema lubrica also exhibits all carpogonial branch features considered by Huisman & Kraft (1994) to be important in defining the genus *Ganonema*: straight carpogonial branches occupying positions of vegetative cortical laterals deep within cortical fascicles and occasional occurrence of both carpogonial branches on adventitious cortical filaments arising from rhizoids and bicarpogonial supporting cells. Young and prefertilized carpogonial branches can be recognized at least to 3 cm from the apex as a consequence of their origin on subsidiary cortical filaments. Possibly, this may be a clear difference between the genera *Ganonema* and *Liagora*. In *Ganonema,* numerous carpogonial branches are formed on mature cortical fascicles and on adventitious filaments, resulting in conspicuous distribution along the young axes. In contrast, in *Liagora* the rhizoids do not form subsidiary cortical filaments, and carpogonial branches are restricted to cortical fascicles close to the apex of the plant, having originated even before the cortical fascicles were fully developed (Desikachary 1956; Desikachary & Balakrishnan 1957; personal observations in *Liagora* species of the Canary Islands).

The number of cells of the carpogonial branch is variable, from five to eight in some unfertilized branches, although six-

Table 1. Comparison of *Ganonema lubrica* with previously described species of *Ganonema* and the Mucosae group of *Liagora*.

Character	G. codii[1]	G. farinosa[2]	G. helminthaxis[3]	G. lubrica
Distribution	South Australia and Victoria	Tropics to warm temperate	Western Australia	Canary Islands
Maximum diameter of medullary cells (μm)	100	180	65	150
Shape of basal cell of cortical fascicles	subisodiametric	subisodiametric	subisodiametric	subcylindrical to clavate
Shape of middle and outer cortical cells	ovoid to moniliform	cylindrical to barrel-shaped	ovoid to barrel-shaped	ellipsoid to moniliform
Cells in carpogonial branch	3–4	4(–6)	(3–)4(–6)	(5–)6(–8)
Diameter of carposporophyte (μm)	150–250	up to 450	up to 300	up to 250
Carposporangia (μm)	8–14 × 20–30	7–15 × 18–40	12–18 × 28–31	10–18 × 15–25
Gonimorhizoids	absent	absent	absent	rare and inconspicuous
Site of derivation of sterile postfertilization filaments	many locations on adjacent assimilatory filaments	many locations on adjacent assimilatory filaments	supporting, infra- and suprasupporting cells	suprasupporting cell
Site of spermatangial branches on cortical fascicles	subterminal or terminal	terminal	terminal	subterminal

[1] Data on *G. codii* (Womersley) Huisman et Kraft from Womersley (1965, as *Liagora codii*).
[2] Data on *G. farinosa* (Lamouroux) Fan et Wang from Tseng (1941, as *Liagora farinosa*) and Kvaternik *et al.* (1996).
[3] Data on *G. helminthaxis* Huisman et Kraft from Huisman & Kraft (1994).

celled carpogonial branches were dominant. This large number of cells forming the carpogonial branch is unusual among species of the *Ganonema*-Mucosae group complex. The more common number of cells in carpogonial branches is reported to be four, but three to six can also occur (Kraft 1989; Huisman & Kraft 1994). Although the number of cells in the carpogonial branch is considered to be a constant generic feature throughout the Liagoraceae (Kraft 1989), the genus *Ganonema* seems to be exceptional. In *Ganonema* the range of variation of this feature has not been determined, and Huisman & Kraft (1994) preferred to consider this feature of no diagnostic value at the genus level. Nevertheless, the number and shape of its individual cells determine the appearance of the carpogonial branch, which is a consistent and useful specific diagnostic character of *Ganonema lubrica*.

Ganonema lubrica exhibits a wide range of variation in the sterile postfertilization filaments associated with the carpogonial branch and the carposporophyte. In the same area of the plant, sterile filaments may be entirely absent, or mature carposporophytes or sterile filaments derived from the suprasupporting cell may be common. Sterile filaments can be short and partially encircle only a portion of the carpogonial branch, or they may be long and curl around all the cells of the carpogonial branch. However, sterile filaments do not surround the gonimoblasts. This variability in the degree of development of sterile filaments seems to be common in carposporophytes of the *Liagora* species belonging to the section Mucosae, which have often been described as either naked or having a few inconspicuous sterile filaments (Desikachary & Balakrishnan 1957), and it supports leaving these features out of the delineation of *Ganonema* (Huisman & Kraft 1994). The new species differs from other species of *Ganonema* and the Mucosae section of *Liagora* in the derivation of most sterile filaments from the suprasupporting cell. In *Ganonema farinosa* (Abbott 1990b, as *Liagora*; Kvaternik *et al.* 1996), *G. codii* (Womersley 1965, as *Liagora*), *Liagora dendroidea* (Desikachary & Balakrishnan 1957, as *L. mucosa*), and *L. sa-*

maensis (Abbott 1984, as *L. amplectens*), sterile filaments have been reported to arise from many locations on adjacent assimilatory filaments. In *Ganonema helminthaxis* (Huisman & Kraft 1994) sterile filaments are initially borne on the supporting cell, then later from cells immediately above and below the supporting cell; in *Liagora pectinata* (Abbott 1990a) sterile filaments arise from cells below the supporting cell; and finally, *L. orientalis* J. Agardh shows sterile filaments derived from both the supra- and infrasupporting cell. Although *L. orientalis* was analyzed by Abbott (1990a) together with species of the Mucosae group, this species shows lateral carpogonial branches and the occurrence of a cell fusion in mature carposporophytes (Doty 1978, as *Izziella abbottiae* Doty).

Ganonema lubrica differs from the other species of *Ganonema* and of the Mucosae group of *Liagora* mainly in the architecture of carpogonial branches, the shape of the basal cell of cortical fascicles, the derivation of most sterile filaments from the suprasupporting cell, and the occasional production of rhizoids from the gonimoblasts (Table 1). This combination of differences appears to justify the description of the Canarian plants as a new species. *Ganonema lubrica* also differs in relatively minor details, such as the diameter of medullary cells, the shape of middle and outer cortical cells, the dimensions of carposporophytes and carposporangia, and the site of spermatangial branches on cortical fascicles (Table 1).

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Table 1. Extended.

L. dendroidea[4]	*L. pectinata*[5]	*L. samaensis*[6]
Caribbean	Bermuda	Hainan Island (China) and Hawaii
70	52	150
subisodiametric	subisodiametric	subcylindrical to clavate
cylindrical to barrel-shaped	ellipsoid to spherical	cylindrical to barrel-shaped
(3–)4	no data	3–6
150–175	100–180	c. 150 [7]
14–18 × 28–38	15 × 31	c. 12 × 20 [7]
absent	absent	absent
many locations on adjacent assimilatory filaments	infrasupporting cell	many locations on adjacent assimilatory filaments
terminal	no data	terminal or subterminal

[4] Data on *L. dendroidea* (P. et H. Crouan in Mazè et Schramm) Abbott from Abbott (1990a) and Desikachary & Balakrishnan (1957, as *Liagora mucosa* Howe).

[5] Data on *L. pectinata* Collins et Harvey from Abbott (1990a).

[6] Data on *L. samaensis* Tseng from Tseng (1941) and Abbott (1984, as *L. amplectens* Abbott).

[7] Based on published illustrations.

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