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Taxonomic notes on the Japanese species of *Gymnogongrus* (Phylloporaceae, Rhodophyta)

Michio MASUDA

Six taxa of the red algal genus *Gymnogongrus* (Gigartinales, Phylloporaceae), *G. flabelliformis* HARVEY, *G. paradoxus* SURINGAR, *G. divaricatus* HOLMES, *G. catenatus* YENDO, *G. japonicus* SURINGAR and *G. furcellatus* var. *japonicus* HOLMES, originally described from Japan were studied on the basis of the type specimens and specimens collected chiefly at the type localities. The first four species can be recognized as distinct taxonomic species and detailed descriptions were given. *G. japonicus* and *G. furcellatus* var. *japonicus* are placed in synonymy with *G. flabelliformis* and *G. paradoxus*, respectively. The important taxonomic features characterizing each species are: (1) the branching intervals and angles contributing to the thallus shape; (2) the thallus width; (3) the number of medullary filaments, the dimension of medullary cells, and the number of anticlinal cortical cell-rows correlating with the thallus texture; (4) the dimension of spermatangia; and (5) the cortical thickness around the cystocarps. The geographical distribution of *G. paradoxus* and *G. catenatus*, which have been confused with each other, is assessed.

The following eight taxa of the red algal genus *Gymnogongrus* (Phylloporaceae) were originally described from Japan: *G. flabelliformis* HARVEY (1856), *G. pinnulatus* HARVEY (1856), *G. ligulatus* HARVEY var. *angustus* HARVEY (1859), *G. japonicus* SURINGAR (1867), *G. paradoxus* SURINGAR (1874), *G. divaricatus* HOLMES (1896), *G. furcellatus* (C. AGARDH) J. AGARDH var. *japonicus* HOLMES (1896) and *G. catenatus* YENDO (1920). Of these, *G. pinnulatus* and *G. ligulatus* var. *angustus* are now known as *Chondrus pinnulatus* (HARVEY) OKAMURA (1930) and *Carpopeltis angusta* (HARVEY) OKAMURA (1910), respectively. These species are not considered further here. *G. paradoxus* was transferred to *Ahnfeltia* (Phylloporaceae) by OKAMURA (1934) and *G. furcellatus* var. *japonicus* was reduced to a synonym of the former species (OKAMURA, 1934). These ascriptions were accepted by MIKAMI (1965). However, there is no reason to include the alga in *Ahnfeltia*. *G. paradoxus* is distinguished from the genus *Ahnfeltia* [type species, *A. plicata* (HUDSON) FRIES] by the formation of internal cystocarps with carpogones and catenate cruciately-divided tetrasporangia originating from intercalary cells of the erect filaments of crustose thalli (MASUDA, 1982). *Ahnfeltia* is characterized by the formation of external pustule-like nemathecia (ROSENVINGE, 1931; GREGORY, 1934; SCHOTTER, 1968; FARNHAM and FLETCHER, 1976) and single zonately-divided tetrasporangia borne terminally on

the erect filaments of crustose thalli (FARNHAM and FLETCHER, 1976; CHEN, 1977). In this article the alga is treated as a species of *Gymnogongrus*.

Of the other four species, *Gymnogongrus flabelliformis* is very common in Japan (OKAMURA, 1936). It has a heteromorphic type life history (MASUDA *et al.*, 1979; MASUDA, 1981) and the vegetative and reproductive features have been reported by OKAMURA (1921, 1936), TOKIDA and MASAKI (1959), MIKAMI (1965) and MASUDA *et al.* (1979). However, a biosystematic study in progress (MASUDA, unpublished) shows that three breeding groups separated reproductively by various isolating mechanisms are present in this taxonomic species. The status of the remaining three species, *G. japonicus*, *G. divaricatus* and *G. catenatus* remain uncertain. MIKAMI (1965), who published a monographic study of Phylloporaceae and Gigartinaceae in Japan, did not mention these species, although CHIHARA (1967) reported *G. divaricatus* as a distinct species. *G. japonicus* has been reported in some floristic publications (NODA, 1964, 1966).

The purpose of the present study is: (1) to compare original material of the six taxa of *Gymnogongrus* with contemporary species concepts; (2) to designate a lectotype specimen when the holotype is absent; and (3) to provide a more detailed description of each taxon on the basis of the type specimen and specimens from the type locality. This will be helpful to our understanding of the genus in Japanese and adjacent waters.

Materials and Methods

Herbarium specimens used for the original descriptions of six taxa of *Gymnogongrus* were examined on loan from the Rijksherbarium, Leiden (L), the British Museum (Natural History) (BM), the Herbarium of Trinity College, Dublin (TCD) and the Herbarium of University Museum, University of Tokyo (TI). Furthermore, historical and contemporary specimens including liquid-preserved specimens deposited in the Herbarium of Faculty of Science, Hokkaido University (SAP) were examined to obtain more detailed data. All these specimens examined will be cited in the description of each taxon. Sections were made by hand using a razor blade and pith stick or using a scalpel (Feather No. 15) under a dissecting microscope, stained with 0.5% (w/v) cotton blue in a lactic acid/phenol/glycerol/water (1:1:1:1) solution and mounted in 50% glycerol-seawater on microscope slides. Voucher slides are deposited in SAP.

Results and Discussion

Gymnogongrus flabelliformis HARVEY

This alga was first described by HARVEY (1856) on the basis of specimens collected at Shimoda, Shizuoka Prefecture in April 1854. His voucher specimens, mounted on two separate sheets, are now conserved in TCD (PARNELL, pers. comm.). One sheet (Fig. 1A) and a picture of the other on loan from TCD were examined with the kind help of Dr. J. PARNELL. Gross morphological features of these specimens are in agreement with the HARVEY's original description. HARVEY did not designate a holotype specimen. As the International Code of Botanical Nomenclature (ICBN) allows the type to consist of more than one individual preserved on one herbarium sheet for

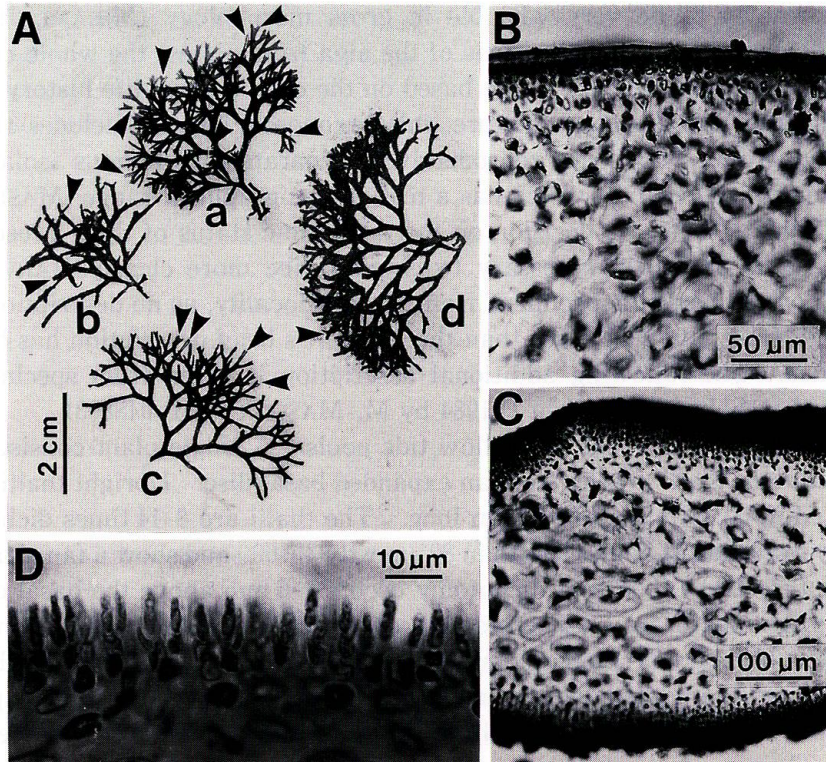


Fig. 1. *Gymnogongrus flabelliformis* HARVEY. A: Lectotype collected at Shimoda, Shizuoka Prefecture in April 1854 (TCD) (arrowheads indicate the positions in which sections were made). B, C: Cross sections of the lectotype; B, the upper portion; C, the middle portion. D: Longitudinal section of the upper portion of the lectotype, showing spermatangia.

small herbaceous plants and for most non-vascular plants (Article 9.1, VOSS *et al.*, 1983), the sheet shown in Fig. 1A is designated here as the lectotype.

HARVEY (1856) did not describe anatomical and reproductive structures of *G. flabelliformis*. Sections were made at several positions on the lectotype (Fig. 1A, arrowheads). The upright thallus is composed of two layers: a medulla of thick-walled, large cells with many pit connections between adjacent cell rows and a cortex of thin-walled, small cells with less frequent pit connections between adjacent cell rows (Fig. 1B, C). Three of the four upright thalli examined possessed spermatangia (Fig. 1A, a-c) and the remaining (Fig. 1A, d) was vegetative. One or two spermatangia are formed from a single spermatangial parent cell in a sorus (Fig. 1D). Mature spermatangia are anticlinally elongated and 9-10 μm long \times 2.5-3.0 μm wide.

This alga has been recorded from both coasts of Pacific and Sea of Japan and is known to be very variable in gross morphology (MIKAMI, 1965). According to my recent collections of the alga from almost the whole coast of Japan and biosystematic study based on the comparative life history and hybridization in laboratory culture, this taxonomic species includes three breeding groups which are reproductively separated by various isolating mechanisms and each of which has a distinct geographical range (MASUDA, unpublished). Before a decision on the taxonomic status of these breeding groups, it is obviously necessary to circumscribe more clearly HARVEY's species on the basis of specimens from its type locality, as no description of this alga from Shimoda other than the HARVEY's brief description has been published. The following additional description is given from specimens collected at Shimoda on June 1, 1984 by M. MASUDA (SAP 048803).

Plants grow on rocks in shallow tide pools. A single plant consists of many upright thalli arising from an expanded basal disc. Upright thalli are dark red in color and up to 5.5 cm long. The thalli are 8-14 times dichotomously branched at angles less than 80° (mostly 40-60°) and show a fan-shaped outline (Fig. 2A). The first dichotomy occurs 1-6 mm above the basal disc. The upright thalli are only terete just above the basal disc, 550-800 μm in diameter, abruptly becoming compressed upward, and are 400-480 μm thick at the lower to middle portions and 290-400 μm thick 5 mm below the apex. They are narrowly linear, but they become slightly broader toward each fork. They reach a maximum width of 1.1-1.3 mm at the lower to middle portions except at forks of 1.5-3.0 mm wide, then gradually becoming narrower and are 800-950 μm wide 5 mm below the apex. Proliferations develop from both margins of the lower to middle portions of upright thalli.

Medullary filaments of the upright thalli are 18-20 rows at the lowest

terete portion and 12-15 rows at the lower to upper portions. The medullary cells are elliptical to angular in longitudinal section (Fig. 2B) and $75\text{--}200\ \mu\text{m}$ long \times $30\text{--}70\ \mu\text{m}$ thick in the center of the medulla at the lower to upper portions. Smaller cells, $25\text{--}50\ \mu\text{m}$ long \times $15\text{--}20\ \mu\text{m}$ thick, are interspersed among these cells. The medullary cells are elliptical in cross section (Fig. 2C) and $40\text{--}110\ \mu\text{m}$ wide \times $30\text{--}70\ \mu\text{m}$ thick in the center of the medulla at the lower to upper portion. Smaller cells, $20\text{--}35\ \mu\text{m}$ wide \times $15\text{--}20\ \mu\text{m}$ thick, are interspersed among these cells. The medullary cells become gradually more slender and shorter toward anticlinal cortical filaments. The cortical cells are rectangular and $4\text{--}5\ \mu\text{m}$ wide in the outer cortex and $10\text{--}20\ \mu\text{m}$ wide in the inner cortex. Numbers of anticlinal cortical cell-rows vary according to the parts of a single thallus; 16-24 at the lowest portion, 8-10 at the lower portion and 4-7 at the middle to upper portions. Unicellular colorless hairs

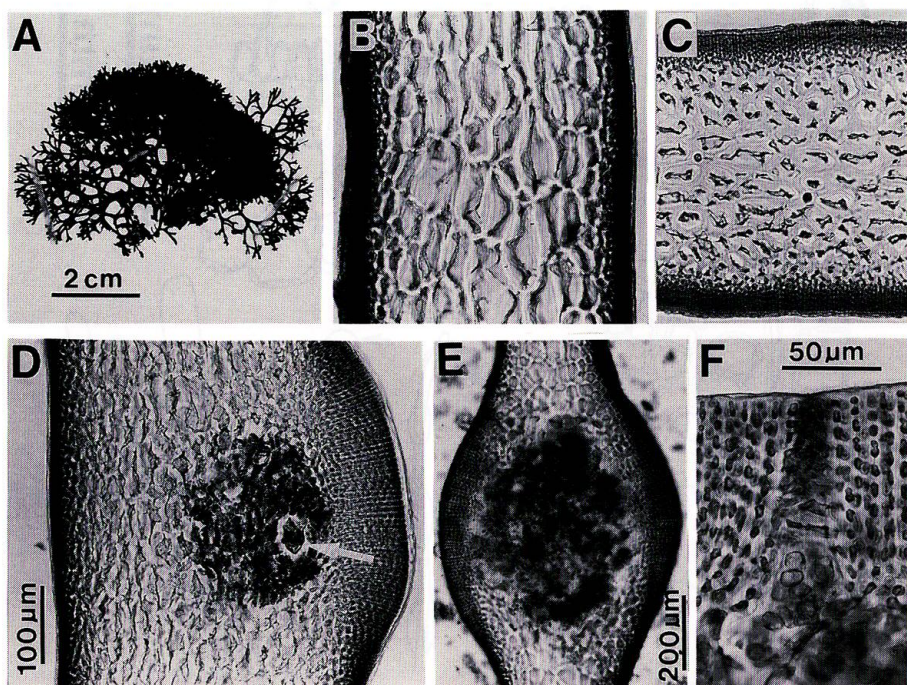


Fig. 2. *Gymnogongrus flabelliformis*. All from specimens collected at the type locality, Shimoda on June 1, 1984. A: Cystocarpic specimen (SAP 048803). B, C: Sections of the middle portion of a thallus; B, longitudinal; C, cross. D: Developing cystocarp (longitudinal section); note a supporting cell (arrow) and the thickened cortex. E, F: Longitudinal sections through a cystocarp; F, showing a carpostome. Scale in D applies also to B and C.

develop from the outermost cortical cells near the apices of male and female gametophytes (Fig. 3A, C).

Spermatangia are identical with those of the lectotype specimen as shown in Fig. 3A, B. Procarps are formed in groups at the uppermost portion of branches. Each procarp consists of a large supporting cell and a three-celled carpogonial branch (Fig. 3C, D). Two sterile cells develop from the first cell of the carpogonial branch (Fig. 3C, D). Cortical cells near a supporting cell beginning to form gonimoblasts are repeatedly divided (Fig. 2D). Later, cortical cells of the opposite side are also divided. The cortical cells of both sides build up a thickened cortex around the developing cystocarp except both margins which are slightly thicker than the adjacent vegetative parts.

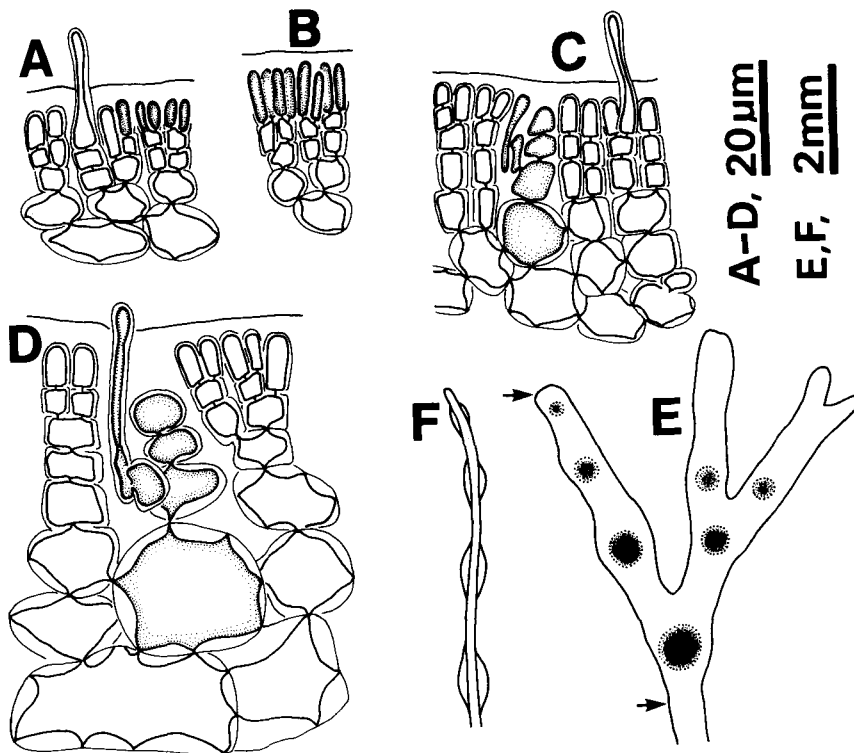


Fig. 3. *Gymnogongrus flabelliformis*. All from specimens collected at Shimoda on June 1, 1984. A, B: Development of spermatangia (longitudinal section); note a colorless hair in A. C, D: Development of procarps (longitudinal section); note a colorless hair in C. E, F: Cystocarpic branch; E, surface view; F, lateral view of the portion between two arrows in E.

Cystocarps are formed on ultimate and penultimate branches in catenate series of 3-5 (Fig. 3E, F). Mature cystocarps are 500-600 μm long, 400-550 μm wide and 300-500 μm thick. The cortex near the supporting cell is usually slightly thicker than on the opposite side. The former is composed of 10-14 cell-rows and is 100-130 μm thick, whereas the latter is composed of 7-11 cell-rows and is 60-100 μm thick. The cortex of adjacent vegetative parts is composed of 4-6 cell-rows and is 25-40 μm thick. The cystocarpic parts, therefore, are prominent (Fig. 2E, 3F) and 580-700 μm thick, while the adjacent vegetative parts are 220-350 μm thick. The cystocarps are provided with multiple carpostomes in the thickened cortex, through which carpospores are discharged. The carpostome is composed of short periclinal filaments developing from anticlinal filaments and the small cavity (Fig. 2F).

Plants with a similar morphology are widely distributed along the Pacific and Sea of Japan coasts. These plants form one of the three breeding groups found recently in this taxonomic species (MASUDA, unpublished). Plants reproducing under short-day regimes and growing chiefly along the coast of Sea of Japan belong to a second breeding group. Furthermore, plants distributed in the northern area, chiefly along the coast of Hokkaido form a third group. Detailed data on these breeding groups will be presented elsewhere.

Gymnogongrus japonicus SURINGAR

This alga was first described by SURINGAR (1867) from material received from Japan, although the locality is unknown. OKAMURA (1921) reduced the alga to a synonym of *G. flabelliformis*, but he later recognized it as a distinct species (OKAMURA, 1936). SURINGAR'S voucher specimens are now deposited in L. These were examined on loan with the kind help of Dr. W. F. PRUD'HOMME VAN REINE. Two different algae are designated as "TYPE!" on the Leiden sheet (No. 943. 85. 36). One of these is a single specimen and fits well with SURINGAR'S (1870) illustrations of the habit (Fig. 4A) and anatomy (Fig. 4B, C). The other has a sparsely branched thallus and rounded medullary cells. Furthermore, the thallus is redder in color. The former specimen (Fig. 4A) is designated here as the lectotype.

The lectotype specimen lacks the lowest portion. Its habit, however, resembles that of *G. flabelliformis*. The upright thallus is 1.0-1.2 mm wide and 400-450 μm thick at the middle portion and 0.8-1.0 mm wide and 280-380 μm thick 5 mm below the apex except at forks which are slightly broader. Proliferations develop from both margins and surface of the middle portion of the thallus. Sections were made at several positions (Fig. 4A, arrow-

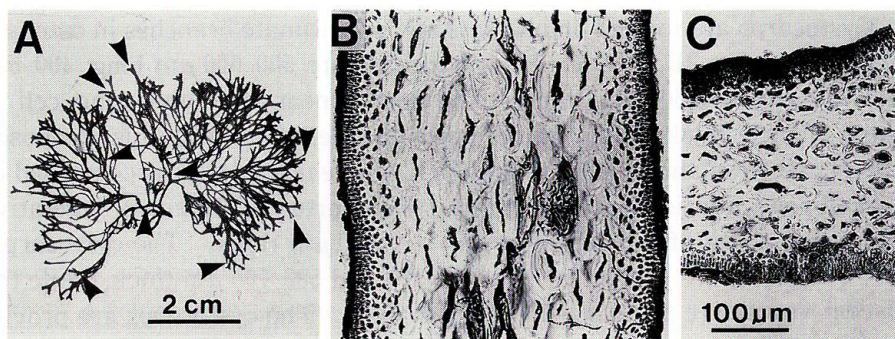


Fig. 4. *Gymnogongrus japonicus* SURINGAR. A: Lectotype in L (arrowheads indicate the positions in which sections were made). B, C: Sections of the middle portion of the lectotype; B, longitudinal; C, cross; note the presence of a filamentous endophytic alga in the medulla. Scale in C applies also to B.

heads), but reproductive structures were not observed. Medullary cells of the thallus are elliptical or angular in longitudinal section (Fig. 4B) and $75\text{--}150\ \mu\text{m}$ long \times $30\text{--}75\ \mu\text{m}$ thick in the center of the medulla at the middle to upper portions. Smaller cells, $20\text{--}50\ \mu\text{m}$ long \times $13\text{--}20\ \mu\text{m}$ thick, are interspersed among these cells. The medullary cells are elliptical in cross section (Fig. 4C) and $50\text{--}110\ \mu\text{m}$ wide \times $30\text{--}75\ \mu\text{m}$ thick in the center of the medulla at the middle to upper portions. Smaller cells, $20\text{--}35\ \mu\text{m}$ wide \times $13\text{--}20\ \mu\text{m}$ thick, are also interspersed among these cells. Cortical cells are in 4–7 anticlinal rows at the middle to upper portions and $4\text{--}5\ \mu\text{m}$ wide in the outer cortex and $10\text{--}20\ \mu\text{m}$ wide in the inner cortex.

The thallus width, the dimension of medullary cells and the number of anticlinal cortical filaments mentioned above show a close similarity between *G. japonicus* and *G. flabelliformis*. SURINGAR's original characterization is not clear, although SURINGAR might distinguish narrow plants from *G. flabelliformis*. Thus, *G. japonicus* SURINGAR (1867) should be reduced to a synonym of *G. flabelliformis* HARVEY (1856). According to OKAMURA (1936), *G. japonicus* is distinguished from the closely related species *G. flabelliformis*, by having narrow axils and slender branches ($1\text{--}1.5\ \text{mm}$ wide) which are irregularly dichotomous and congregated. These features, however, are found in the variation range of *G. flabelliformis*. NODA (1964, 1966) distinguished his *G. japonicus* from *G. flabelliformis* by the absence of proliferations. Since the lectotype of *G. japonicus* possesses proliferations, his distinction has no taxonomic significance.

Gymnogongrus paradoxus SURINGAR

This species was first described with its old Japanese name, Hachijo-funori (as Hatsi-sjoo-funori) by SURINGAR (1874) on the basis of material collected in Japan. The Japanese name suggests that the locality was Hachijo Island. According to SURINGAR (1874), the Hachijo-funori included three or four species at that time. Dried materials were sent to Edo (the old name for Tokyo) and used to size cloth. YENDO (1911) stated that *G. paradoxus* was collected from Hachijo Isl. and Kozu Isl., exported to Honshu, and used as a seaweed glue to size silk in Tokyo and Yamanashi Prefecture, but that in recent times its supply had been less because of a decrease in yield. OKAMURA (1934) transferred this alga to *Ahnfeltia* on account of its anatomical features. According to OKAMURA (1934), medullary cells of *Gymnogongrus* are large and mixed with smaller cells, whereas those of *Ahnfeltia* are smaller and of almost uniform size in older parts of the thallus. This transfer, however, cannot be acceptable, as mentioned in the

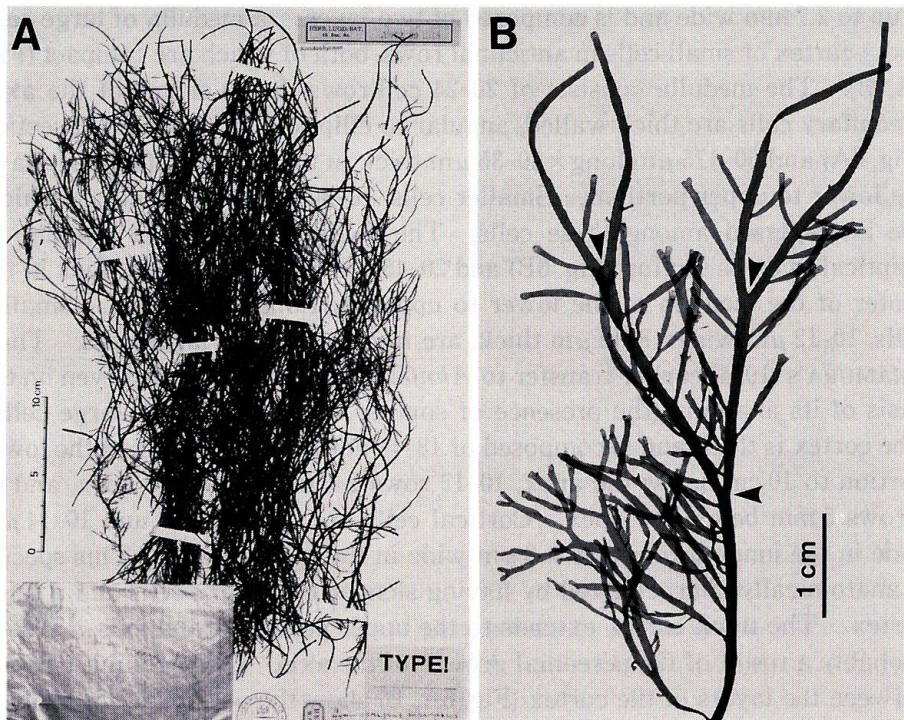


Fig. 5. *Gymnogongrus paradoxus* SURINGAR. A: Holotype in L. B: Portion of the holotype (spermatangial), showing three dichotomous branchings (arrowheads) and many proliferations with constricted bases.

Introduction.

SURINGAR's (1874) original description and illustrations clearly show the taxonomic features of this species. In order to obtain more data of vegetative and reproductive structures his voucher specimens deposited in L (No. 942. 69. 48) were examined on loan with the kind help of Dr. W. F. PRUD' HOMME VAN REINE. Many upright thalli are mounted on the type sheet (Fig. 5A). Both cystocarpic and spermatangial thalli are included. They cannot, however, be separated from each other without severely damaging the plants. These female and male gametophytic thalli should be treated as the holotype according to Article 9.1 of ICBN (VOSS *et al.*, 1983), and they fit well with the original illustrations. The thalli are about 40 cm long (as they are entangled and folded in two, it is impossible to measure the length exactly). Each thallus has a sparsely branched, compressed axis from which many proliferations develop as if they filled the intervening space between branches (Fig. 5B). This is the most distinctive feature of *G. paradoxus* in gross morphology as shown in SURINGAR's (1874) original illustrations. The axis is up to 2.7 mm wide and is composed of two layers: a medulla of large cells and a cortex of small cells in anticlinal rows, both of which are compact (Fig. 6A, B). The medulla consists of 20-24 cell-rows in the center of the axis. Medullary cells are thick-walled, angular to elliptical in longitudinal section (Fig. 6A) and 50-175 μm long \times 20-35 μm thick in the center of the medulla at the lower to upper portions. Smaller cells, 10-30 μm long \times 10-15 μm thick, are interspersed among these cells. The medullary cells are circular to elliptical in cross section (Fig. 6B) and 20-45 μm wide \times 20-35 μm thick in the center of the medulla at the lower to upper portions of the axis. Smaller cells, 10-12 μm wide \times 8-12 μm thick, are frequent among large cells. Thus, OKAMURA's (1934) earlier transfer to *Ahnfeltia* cannot be justified even on the basis of its anatomy (the presence of smaller cells mixed with large cells). The cortex is thick and is composed of 18-44 anticlinal cell-rows at the lower portion to 10 cm below the apex, 10-12 rows 2-5 cm below the apex, and 6-8 rows 5 mm below the apex. Cortical cells are rectangular and 10-14 μm wide in the inner cortex and 4-8 μm wide in the outer cortex. This species is anatomically characterized by having slender medullary cells and a thick cortex. The thick cortex extends to the upper portion of the axis. This is probably a result of the perennial growth of the axis. Distinct limiting lines between the layers of the cortex (Fig. 6A, B) show the periodicity of growth. Proliferations are constricted at the proximal portion and may be distinguished as such from axial dichotomies (Fig. 5B). Secondary proliferations sometimes issue from these primary proliferations. In this case the primary

proliferations have one or two distinct growth rings within their cortex.

One to four cystocarps are formed on short proliferations. They are 650–900 μm long, 650–800 μm wide and 300–600 μm thick. The cortex around the cystocarp except both margins are much thicker than adjacent vegetative parts (Fig. 6C). The thickened parts are 110–150 μm thick and are composed of 12–16 anticlinal cell-rows (the cortex of one side is slightly thicker than the opposite side), but vegetative parts are 30–40 μm thick and composed of 5–6 anticlinal cell-rows. The cystocarpic parts are conspicuously prominent and 600–700 μm thick, while the adjacent vegetative parts are 240–400 μm thick. The cystocarps are provided with multiple carpostomes in the thickened cortex (Fig. 6D).

Spermatangia are formed in a sorus near the apices of proliferations. One or two anticlinally elongated spermatangia are borne terminally on a spermatangial parent cell (Fig. 6E). Mature spermatangia are 12–15 μm long and 2.5–3.0 μm wide.

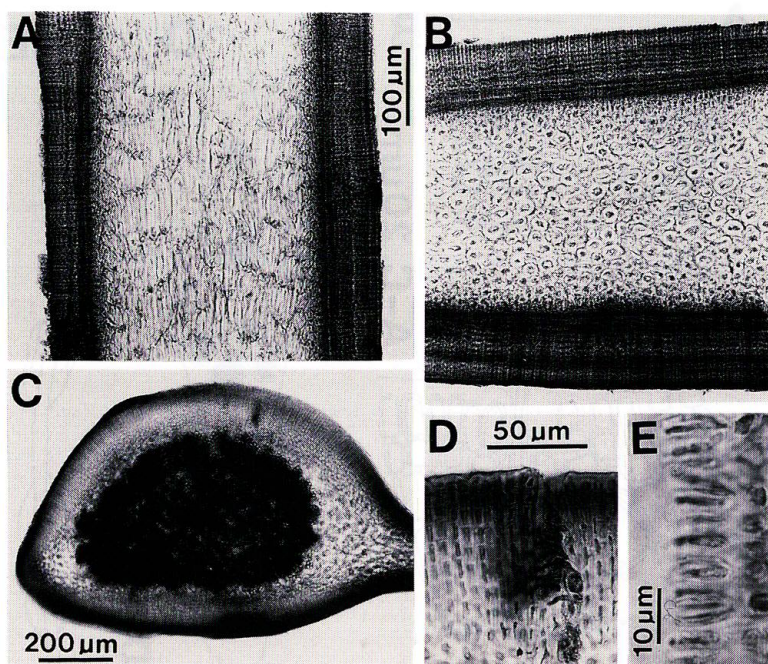


Fig. 6. *Gymnogongrus paradoxus*. All from the holotype. A, B: Sections of the upper portion of the axis (10 cm below the apex); A, longitudinal; B, cross. C, D: Cross sections of a cystocarp; D, showing a carpostome. E: Longitudinal section of a proliferation, showing spermatangia. Scale in A applies also to B.

It would appear that the type locality of *G. paradoxus* is Hachijo Island (SURINGAR, 1874 ; YENDO, 1911). On a recent visit to this island, however, no plants referable to *G. paradoxus* could be found at Okataura, Okago ; Aigae, Nakanogo ; Borawazawa, Sueyoshi ; or Sokodo, Mitsune. This species was found growing abundantly in the intertidal zone at Ako, Okubo and Miike in Miyake Island situated about 100 km to the north of Hachijo. These plants are 30–60 cm long and similar to the holotype in gross morphology and anatomy. It seems possible that SURINGAR received *G. paradoxus* collected from one of the Izu Seven Islands including Hachijo, Miyake and Kozu Isl. Some supplementary data from the Miyake plants are given below. Vouchers of these plants will be cited later in the description of the geographical distribution. Younger portions of upright thalli are coral red in color, but older portions become dark red as the cortex becomes thickened. Spermatangial sori can be distinguished from vegetative parts by their paler color in living specimens. The development and size of spermatangia are similar to

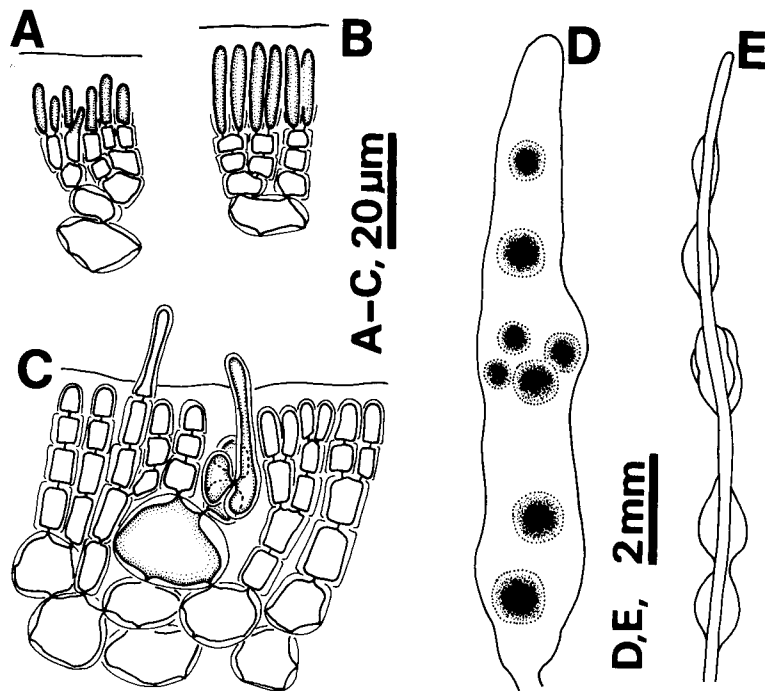


Fig. 7. *Gymnogongrus paradoxus*. All from specimens collected at Ako, Miyake Island on June 26, 1986. A, B: Development of spermatangia (longitudinal section of a proliferation). C: Procarp (longitudinal section of a proliferation); note a colorless hair. D, E: Cystocarpic proliferation; D, surface view; E, lateral view of D.

those of the holotype as shown in Fig. 7A, B. Procarps are formed in groups on the apices of proliferations. Each procarp consists of a large supporting cell, a three-celled carpogonial branch and a one-celled sterile branch produced from the first cell of the carpogonial branch (Fig. 7C). Unicellular colorless hairs develop from the outermost cortical cells near the procarp (Fig. 7C). Cystocarps are usually formed in longitudinal series, but they are sometimes formed in small groups on broad parts of proliferations (Fig. 7D, E).

This species is characterized by having sparsely branched, elongated upright axes with many reproductive proliferations, slender medullary cells and a thick cortex. According to MIKAMI (1965), this alga is exceedingly variable in gross morphology. However, plants with a laxly flabellate habit and narrow thalli (less than 1 mm wide except at forks) should be excluded from the present circumscription of *G. paradoxus* as will be mentioned later for *G. catenatus*. Nevertheless, the thallus habit is not uniform. Various forms are due to the degree of elongation of upright axes and the stage of development of proliferations. Plants with elongated axes and short proliferations (Fig. 8A) look very different from those with less elongated axes and well-developed proliferations (Fig. 8B).

According to OKAMURA (1936), *G. paradoxus* is widely distributed in Japan ranging from Kyushu to northern Honshu. Its records from southerly localities will be dis-

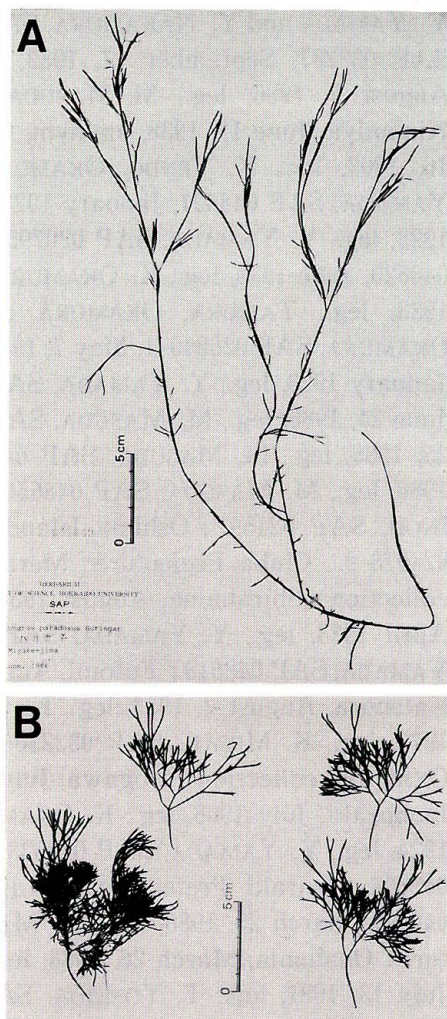


Fig. 8. *Gymnogongrus paradoxus*. A: Spermatangial specimen collected at Okubo, Miyake Island on June 25, 1986 (SAP 048649). B: Specimens collected at Oarai, Ibaraki Prefecture on March 25, 1986 (SAP 048642).

counted (see the section of *G. catenatus*). The present known range of *G. paradoxus* is shown in Fig. 9 on the basis of herbarium specimens deposited in SAP. These are as follows. Mie Prefecture: Ujijamada, March 27, 1929, leg., K. OSHIMA, OKAMURA collection. Shizuoka Prefecture: Omaezaki, September 16, 1982, leg., M. MASUDA, SAP 048640; Shimoda, April 1938, leg., Y. YAMADA and Y. NAKAMURA, SAP 024038, April 3, 1981, leg., M. MASUDA, SAP 032237, September 17, 1982, leg., M. MASUDA, SAP 032238; Atami, August 5, 1986, leg., M. MASUDA, SAP 048652. Kanagawa Prefecture: Ninomiya, June 12, 1938, anonym, OKAMURA collection; Enoshima, January 16, 1903, leg., K. YENDO, OKAMURA collection, November 1922, leg., Y. YAMADA, SAP 048621, January 1923, leg., Y. YAMADA, SAP 048622, October 1923, leg., Y. YAMADA, SAP 020795, December 1923, leg., Y. YAMADA, SAP 048620, June 1933, leg., K. OKAMURA, OKAMURA collection; Koyurugi, April 1933, leg., TAMURA, OKAMURA collection; Misaki, July 1932, leg., K. OKAMURA, SAP 020840-1, May 7, 1944, leg., T. SEGI, SAP 024937; Jogashima, January 1923, leg., Y. YAMADA, SAP 048618. Tokyo: Aoko, Miyake Island, June 24, 1986, leg., M. MASUDA, SAP 048646-7; Okubo, Miyake Island, June 25, 1986, leg., M. MASUDA, SAP 048648-9; Miike, Miyake Island, June 25, 1986, leg., M. MASUDA, SAP 048650-1; Shikine Island, August 1939, leg., S. INOH, SAP 021597; Oshima Island, April 1938, leg., Y. NAKAMURA, SAP 024078-9. Chiba Prefecture: Mera, April 12, 1928, leg., KATO, OKAMURA collection; Shirahama, August 1934, leg., T. MURAOKA, SAP 019952; Emi, April 1923, leg., Y. YAMADA, SAP 048624; Amazura, April 1923, leg., Y. YAMADA, SAP 048619; Futomi, August 1933, leg., T. MURAOKA, SAP 020038; Katsuura, August 2, 1933, leg., K. OKAMURA, OKAMURA collection, July 22, 1978, leg., K. MIYAJI, SAP 032230; Ohara, July 31, 1932, leg., F. HIRAGA, OKAMURA collection; Togawa, July 18, 1985, leg., M. MASUDA, SAP 048641; Inubozaki, July 1906, leg., K. OKAMURA, OKAMURA collection, February 11, 1924, leg., Y. YAMADA, SAP 048623, March 29, 1982, leg., M. MASUDA, SAP 048806. Ibaraki Prefecture: Oarai, August 5, 1956, leg., Y. TSUJI, SAP 048805, March 25, 1986, leg., M. MASUDA, SAP 048642. Fukushima Prefecture: Onahama, March 26, 1986, leg., M. MASUDA, SAP 048644; Nagasaki, July 13, 1981, leg., T. YOSHIDA, SAP 035859, 043824; Toyoma, August 13, 1932, leg., KATAZAKI, OKAMURA collection; Shioyazaki, March 26, 1986, leg., M. MASUDA, SAP 048643; Yotsukura, August 5, 1933, leg., KATAZAKI, OKAMURA collection, March 26, 1986, leg., M. MASUDA, SAP 048645. Miyagi Prefecture: Hanabuchi, April 17, 1950, leg., M. KUROGI, SAP 025726; Sabusawa, August 19, 1967, leg., T. YOSHIDA, SAP 035230; Onagawa, June 1942, leg., S. INOH, SAP 023400; Enoshima, August 29, 1920, leg., K.

OKAMURA, OKAMURA collection. Iwate Prefecture: Rikuzentakada, October 1, 1980, leg., T. YAMAMOTO, SAP 048560; Hirota, June 1954, leg., S. KAWASHIMA, SAP 027804; Ofunato, May 21, 1951, leg., S. KAWASHIMA, SAP 027087; Kamaishi, August 18, 1951, leg., S. KAWASHIMA, SAP 027089; Otsuchi, March 28, 1979, leg., M. MASUDA, SAP 032231-4, May 16, 1983, leg., R. YAMANISHI, SAP 048561; Miyako, April 12, 1951, leg., S. KAWASHIMA, SAP 027085; Kuji, August 17, 1982, leg., S. YOSHIDA, SAP 048807; Nakano, July 20, 1951, leg., S. KAWASHIMA, SAP 027086, July 1, 1954, leg., S. KAWASHIMA, SAP 027877; Shukunohe, May 7, 1966, leg., T. YOSHIDA, SAP 035072. Aomori Prefecture: Same, August 1940, leg., S. INOH, SAP 021809, July 28, 1979, leg., M. MASUDA, SAP 032235-6; Shimofuro, August 1940, leg., S. INOH, SAP 021811.

This species is distributed along the Pacific coast of Japan ranging from Mie to Aomori Prefecture. OKAMURA (1936) recorded this alga from a more

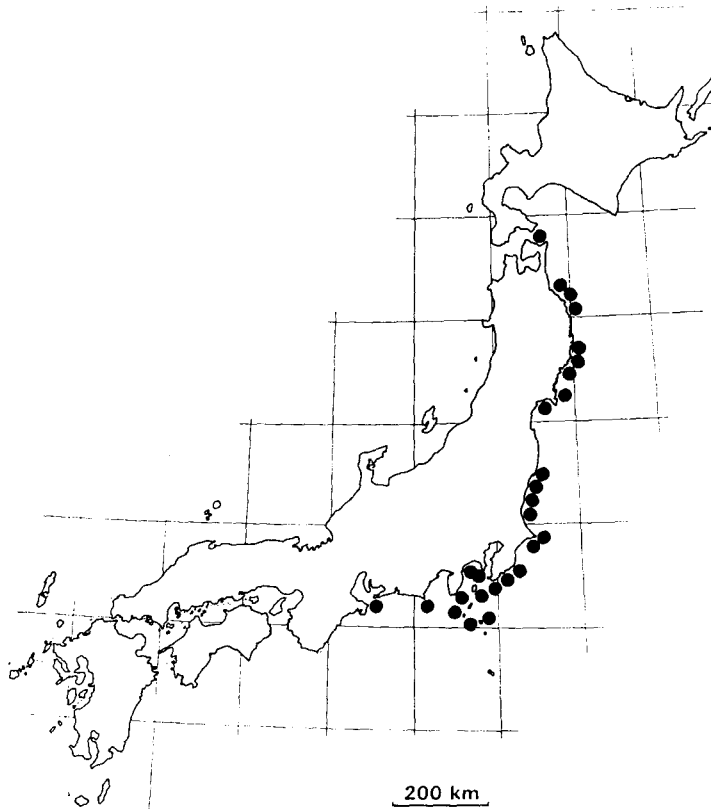


Fig. 9. Distribution of *Gymnogongrus paradoxus*, compiled from specimens in SAP.

southerly area, Ehime Prefecture, and from a single locality on the coast of Sea of Japan, Ajigasawa, Aomori Prefecture. His voucher specimens of these records are included in his collection (SAP). The Ehime specimens collected by S. YAGI (locality not known) are referable to *G. paradoxus*, although the Ajigasawa specimen collected by Y. MURAKAMI cannot be identified with certainty. The lack of confirmed records from adjacent areas requires a further study of the alga *in situ*.

Gymnogongrus divaricatus HOLMES

This species was first described by HOLMES (1896) from material collected at Shimoda in March 1894 (SAIDA No. 61a). The holotype specimen is now deposited in BM (Fig. 10A). This specimen on loan from BM was examined with the kind help of Mrs. L. M. IRVINE. The original description given by HOLMES (1896) clearly shows gross morphological features of this species. Upper branches and proliferations of the thallus are pale red in color and the lower parts are dark red in color, as described by HOLMES (1896). As the specimen was collected almost a century ago, its color is probably somewhat faded. The color, however, is essentially similar to that of plants growing in the lower intertidal to upper subtidal zones at Shimoda,

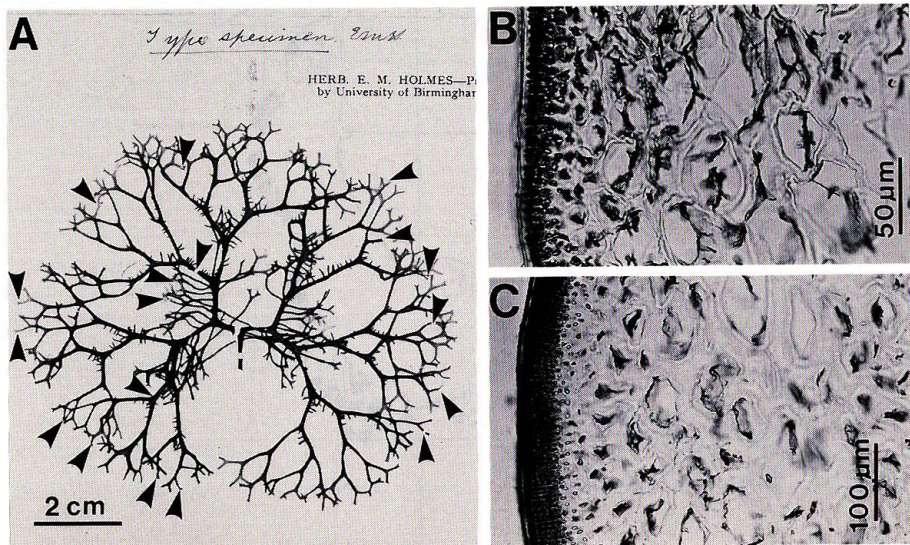


Fig. 10. *Gymnogongrus divaricatus* HOLMES. A: Holotype collected at Shimoda in March 1894 (BM) (arrowheads indicate the positions in which sections were made). B, C: Cross sections of the holotype; B, the upper portion; C, the middle portion.

the type locality. This species can be discriminated at first sight from the closely related *G. flabelliformis* by this color in their sympatric field. Longitudinal and cross sections were made at many positions of the holotype (Fig. 10A, arrowheads), but no reproductive structures were detected. Medullary cells are large, as reported by HOLMES (1896). They are elliptical in cross section and 70-130 μm wide \times 40-90 μm thick at the upper portion (Fig. 10B) and 90-160 μm wide \times 60-110 μm thick at the middle portion (Fig. 10C). Subsequent to HOLMES's brief description, OKAMURA (1934) gave an additional description with several illustrations. These descriptions and illustrations, however, are not adequate to circumscribe this species. The following observation was made on the basis of specimens collected at the type locality on June 1, 1984 by K. MATSUE and M. MASUDA (SAP 048698).

Several upright thalli arise from a common basal disc and are up to 11 cm long. The thalli are 7-13 times dichotomously divided at angles of about 70-90° at the lower to middle portions and at angles of 45-65° at the upper portion and are widely flabellate to almost circular in outline (Fig. 11A, B). The first dichotomy occurs 1-15 mm above the basal disc. The upright thalli are only terete just above the basal disc and 600-900 μm in diameter, abruptly becoming compressed upward and are 500-700 μm thick 2 mm above the basal disc. They are linear, but become slightly broader toward each fork. They attain a maximum width of 2.0-2.5 mm at the lower to middle portions except at forks which are broader than other parts and 3.0-3.5 mm wide. Later they become gradually narrower upward and are 0.9-1.2 mm wide 5 mm below the apex. Many proliferations are issued from the margins (sometimes from the surface) throughout the thallus.

The upright thallus is composed of two layers: a medulla of large, colorless cells and a cortex of small, pigmented cells in anticlinal rows. The medullary cells are thick-walled, closely packed and are joined by many secondary pit connections. The cells are elliptical in longitudinal section (Fig. 11C) and are 100-300 μm long \times 50-110 μm thick in the center of the medulla at the lower to upper portions of the thallus. Smaller cells, 40-70 μm long \times 25-40 μm thick, are interspersed among these large cells. The medullary cells are elliptical to almost circular in cross section (Fig. 11D) and 60-170 μm wide \times 50-110 μm thick in the center of the medulla at the lower to upper portions. Smaller cells, 25-50 μm wide \times 25-40 μm thick, are also interspersed among these cells. The medullary cells become gradually more slender and shorter toward anticlinal cortical filaments. The cortical cells are thin walled, rectangular, closely packed and are joined by a few secondary pit connections. They are 4-8 μm wide in the outer cortex and 10-

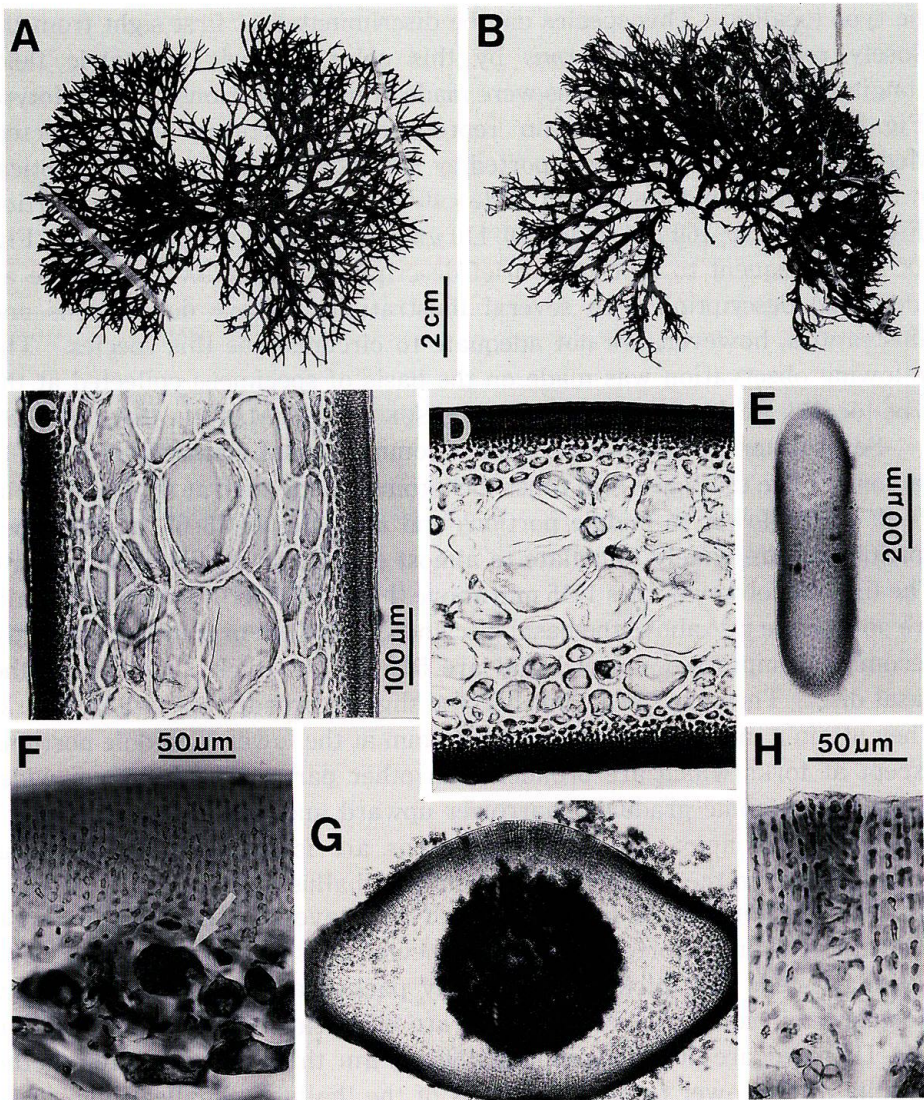


Fig. 11. *Gymnogongrus divaricatus*. All from specimens collected at the type locality, Shimoda on June 1, 1984. A: Cystocarpic specimen (SAP 048698). B: Spermatangial specimen (SAP 048698). C, D: Sections of the middle portion of a thallus; C, longitudinal; D, cross; E, Procarpus formed slightly depressed area just below the apex of a branch (cross section). F: Gonimoblast initials (longitudinal section); note a supporting cell (arrow) and the thickened cortex. G, H: Cross sections through a cystocarp; H, showing a carpostome. Scale in A applies also to B; scale in C applies also to D; scale in E applies also to G.

20 μm wide in the inner cortex. Numbers of cortical cell-rows change according to the parts of a single thallus, although medullary cell-rows are 8-10 throughout the thallus. The cortical cells are in 17-25 rows at the lowest terete portion, 8-11 rows at the lower portion and 5-8 rows at the middle to upper portions. Unicellular colorless hairs develop from the outermost cortical cells near the apical portion of male (Fig. 12A) and female gametophytes.

Reproductive structures are formed on the upper branches and proliferations. Procarys are formed in groups in the center of apices of these branches and proliferations. The procary-bearing area is at first slightly depressed (Fig. 11E). Each procary consists of a large supporting cell and a three-celled carpogonial branch (Fig. 12C, D). Two sterile cells are formed on the first cell of the carpogonial branch (Fig. 12C, D). Cortical cells near a supporting cell that is beginning to form gonimoblasts are repeatedly divided (Fig. 11F).

Cystocarys are formed on ultimate and penultimate branches and proliferations usually in catenate series of 3-6 (Fig. 12E-G) and sometimes individually on short proliferations less than 2 mm in length. Mature cystocarys are 550-750 μm long, 500-950 μm wide and 300-580 μm thick. The cortex around the cystocary except both margins are much thicker than the adjacent vegetative parts. The cortex near the supporting cell bearing gonimoblasts is usually thicker than its opposite side; the former is composed of 8-14 cell-rows and is 90-130 μm thick, whereas the latter is composed of 6-12 cell-rows and is 60-100 μm thick. The cortex of the adjacent vegetative parts is composed of 4-5 cell-rows and is 30-40 μm thick. The cystocaryic parts are conspicuously prominent (Figs. 11G, 12G) and 550-1000 μm thick, while the adjacent vegetative parts are 250-500 μm thick. The cystocarys are provided with multiple carpostomes in the thickened cortex (Fig. 11H).

Spermatangia are formed in a sorus near the apices of branches and proliferations. One or two spermatangia are produced from a single spermatangial parent cell (Fig. 12B). Mature spermatangia are anticlinally elongated and 10-12 μm long \times 2-3 μm wide.

Gymnogongrus divaricatus has the widest branching angles and largest medullary cells of the Japanese species of the genus examined. Furthermore, this alga can be distinguished from the closely related species, *G. flabelliformis* by broader and redder thalli. *G. divaricatus* has been reported from several localities ranging from Wakayama to Kanagawa Prefecture (OKAMURA, 1934, 1936). I have found that this species grows in the lower

intertidal to upper subtidal zones on exposed shores ranging from Izu Peninsula, Shizuoka Prefecture to Boso Peninsula, Chiba Prefecture. *G. divaricatus* and *G. flabelliformis* are sympatric in this region, but the latter

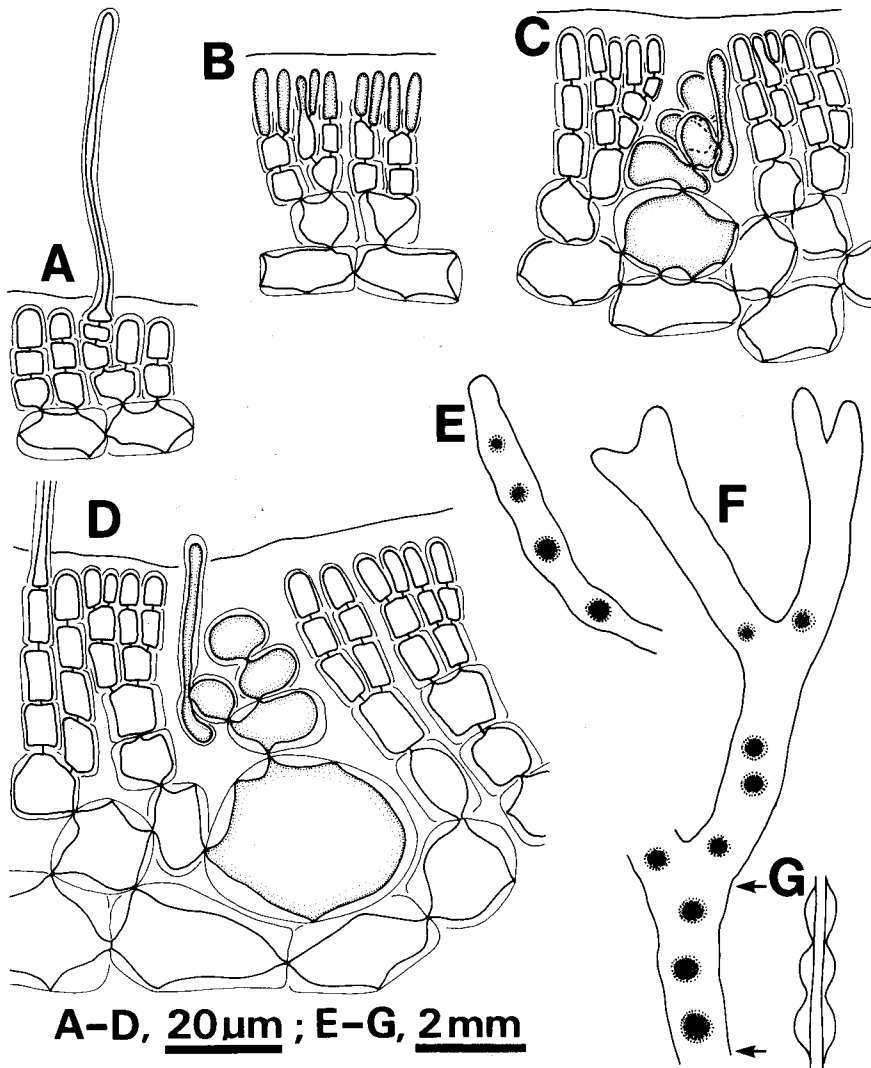


Fig. 12. *Gymnogongrus divaricatus*. All from specimens collected at Shimoda on June 1, 1984. A: Colorless hair on a male gametophyte (longitudinal section). B: Spermatangia (longitudinal section). C, D: Development of procarps (longitudinal section). E: Cystocarpic proliferation (surface view). F, G: Cystocarpic branch; F, surface view; G, lateral view of the portion between two arrows in F.

alga usually grows in tide pools in sheltered places, suggesting that these two species have different ecological preferences. However, *G. flabelliformis* is sometimes found on exposed shores where plants of both species may exist side by side. Further comparative studies of both species are in progress.

Gymnogongrus furcellatus (C. AGARDH) J. AGARDH
var. *japonicus* HOLMES

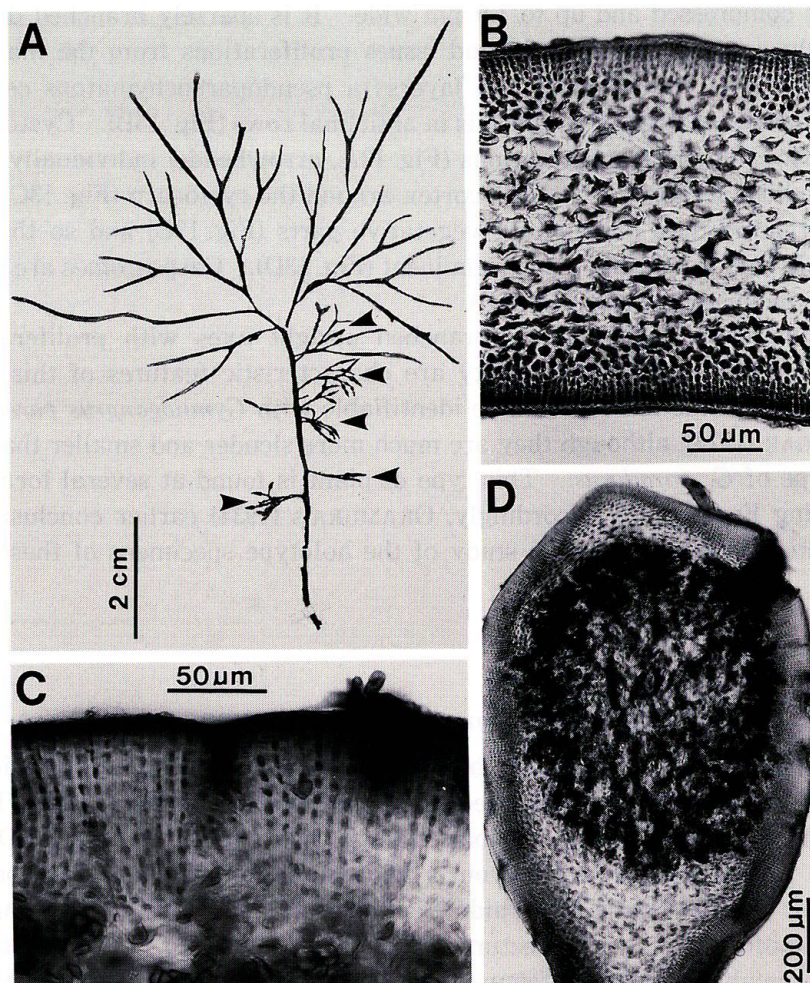


Fig. 13. *Gymnogongrus furcellatus* var. *japonicus* HOLMES. A: Holotype collected at Enoshima, Kanagawa Prefecture in March 1894 (BM) (arrowheads indicate the cystocarpic proliferations). B: Cross section of a cystocarpic proliferation. C, D: Cross section through a cystocarp; C, showing a carpostome.

This alga was first described with a brief description and a habit illustration by HOLMES (1896) from specimens collected at Enoshima, Kanagawa Prefecture in March 1894 (SAIDA No. 34). OKAMURA (1934) stated that this alga has a cylindrical stem, although he placed it in synonymy with *Ahnfeltia paradoxa* (SURINGAR) OKAMURA which has a compressed axis. Re-examination of the HOLMES's original specimens is needed.

The holotype (Fig. 13A) and isotype specimens deposited in BM were examined on loan with the kind help of Mrs. L. M. IRVINE. The upright axis is compressed and up to 1.6 mm wide. It is sparsely branched dichotomously or subdichotomously and issues proliferations from the margins. The thallus is composed of two layers: a pseudoparenchymatous cellular medulla and a cortex of small cells in anticlinal rows (Fig. 13B). Cystocarps are formed in short proliferations (Fig. 13A, arrowheads) individually or in longitudinal series of 2-3. The cortex around the cystocarp (Fig. 13C, D) is much thicker than neighboring vegetative parts (Fig. 13B) and so the cystocarpic part is conspicuously prominent (Fig. 13D). Carpostomes are found in the thickened cortex (Fig. 13C).

Compressed and sparsely branched upright axes with proliferations contributing reproductive activity are characteristic features of this alga. Plants with these features can be identifiable with *Gymnogongrus paradoxus* SURINGAR (1874), although they are much more slender and smaller than the holotype of *G. paradoxus*. This type of plant is found at several localities including Enoshima. Accordingly, OKAMURA's (1934) earlier conclusion is confirmed by a comparative study of the holotype specimens of these two algae.

***Gymnogongrus catenatus* YENDO**

This species was described by YENDO (1920) without the designation of any of types. His voucher specimens are now deposited in TI. These specimens were examined on loan from TI with the kind help of Dr. H. OHBA. They were collected from a wide geographical range in Japan as follows: (1) Fukuyama, Hokkaido, September 21, 1917, leg., L. ROSENBAUM; (2) Shimofuro, Aomori Prefecture, September 2, 1917, leg., L. ROSENBAUM; (3) Horotsuki, Aomori Prefecture, October 5, 1917, leg., L. ROSENBAUM; (4) Ajigasawa, Aomori Prefecture, August 26, 1917, leg., T. TOMOMICHI; (5) Oga Peninsula, Akita Prefecture (date not shown), leg., Y. KUDO; (6) Towa, Niigata Prefecture, July 18, 1915, leg., M. NAKAMURA*; (7) Niigata Pre-

fecture (locality not shown), July 1908, leg., M. NAKAMURA (No. 83), August 1910, leg., R. KOBAYASHI (Nos. 28, 53*); (8) Makiya, Tottori Prefecture, July 23, 1918, leg., Y. IKOMA* ; (9) Fukuoka Prefecture (locality and date not shown), leg., Y. OGURA* ; (10) Amakusa, Kumamoto Prefecture (date not shown) leg., D. KOBAYASHI* ; (11) Kaminada, Ehime Prefecture (date not shown), leg., K. KOMATSUZAKI* ; (12) Gunchu, Ehime Prefecture (date not shown), leg., K. KOMATSUZAKI* ; and (13) Ijika, Mie Prefecture, March 22, 1894, leg., K. YENDO*. These specimens (except those from Shimofuro and Horotsuki) are cited by YENDO (1920). They are treated as the syntypes and one of them must be chosen as a lectotype according to Article 7.7 and T. 4 (c) of Guide for the determination of types of ICBN (VOSS *et al.*, 1983).

This species was originally characterized as having cystocarps formed on terminal elongated branches in prominent longitudinal series (YENDO, 1920). Specimens labeled with an asterisk in the preceding paragraph have cystocarps in catenate series of 2-12 on ultimate and penultimate branches. Morphological and anatomical examinations of YENDO's voucher specimens, however, reveal that his *G. catenatus* includes different entities. One of the cystocarpic specimens which is quoted as (13) in the preceding paragraph is designated here as a lectotype (Fig. 14), and the following description is given on the basis of this specimen.

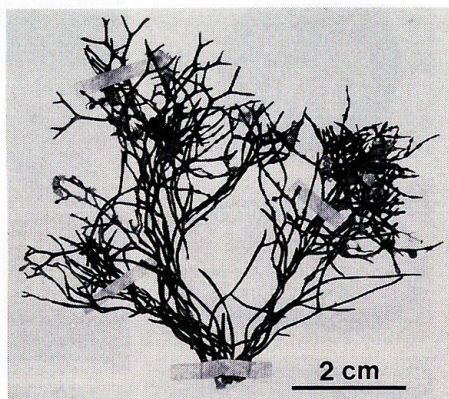


Fig. 14. Lectotype of *Gymnogongrus catenatus* YENDO collected at Ijika, Mie Prefecture on March 22, 1894 (TD).

Several upright thalli issue from a common basal disc, are up to 7 cm long, and are naked at the lower portion (8-15 mm above the basal disc). The thalli are 6-10 times dichotomous at angles of 40-80° at the lower to middle portions and at angles of 60-90° at the upper portion and are laxly flabellate in outline. They are terete (Fig. 15A), 600 μm in diameter just above the basal disc and gradually become compressed upward (Fig. 15B, C). They are narrowly linear, but become slightly broader toward each fork. They are 800-950 μm wide and 300-500 μm thick except at forks of 1.2-1.5 mm wide. A few proliferations develop from the lower portions of thalli. Ultimate branchlets are variable in length according to their developmental stages, 0.5-12.5 mm long and have obtuse apices.

The upright thallus is composed of two layers: a medulla of large cells and a cortex of small cells in anticlinal rows (Fig. 15E, F). The medulla consists of closely appressed filaments of thick-walled cells with many secondary pit connections between adjacent cell-rows. The cells are in 26–30 rows at the lowest terete portion and 18–22 rows at the lower to upper portions. They are angular to elliptical in longitudinal section (Fig. 15F) and $50\text{--}165\ \mu\text{m}$ long \times $15\text{--}35\ \mu\text{m}$ thick in the center of the medulla at the lower to upper portions of the thallus. Smaller cells of $15\text{--}40\ \mu\text{m}$ long \times $10\text{--}12\ \mu\text{m}$ thick are interspersed among these cells. The medullary cells are elliptical to circular in cross section (Fig. 15D, E) and $20\text{--}40\ \mu\text{m}$ wide \times $15\text{--}35\ \mu\text{m}$ thick

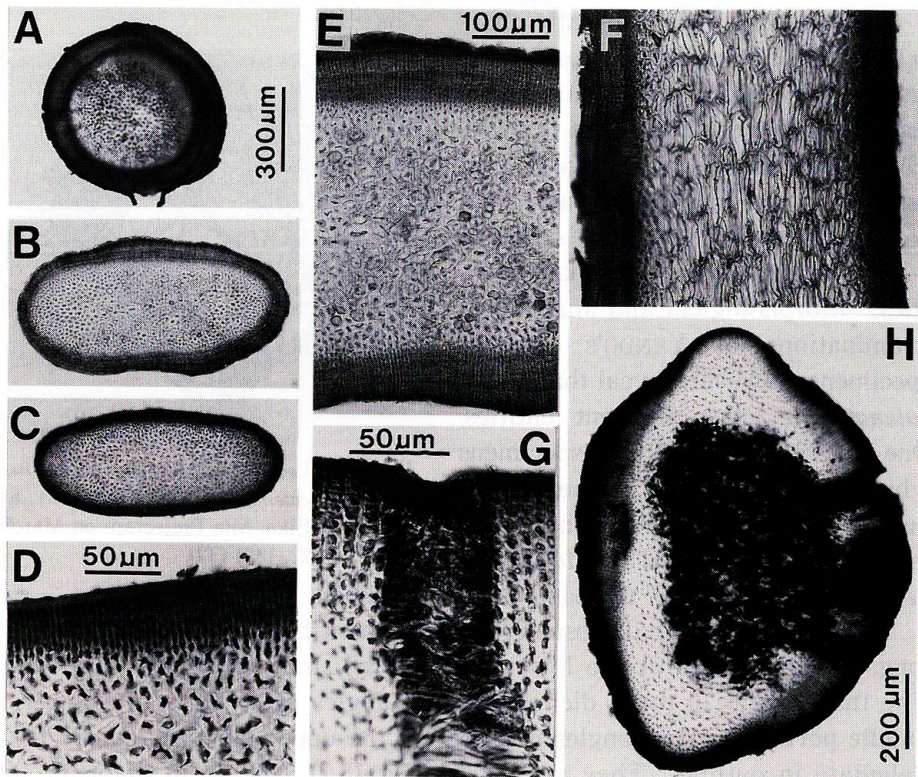


Fig. 15. *Gymnogongrus catenatus*. All from the lectotype specimen. A-E: Cross sections of the upright thallus; A, the lower terete portion; B, E, the middle portion; C, D, the upper portion (5 mm below the apex). F: Longitudinal section of the middle portion. G, H: Cross section through a cystocarp; G, showing a carpostome. Scale in A applies also to B and C; scale in E applies also to F.

in the center of the medulla at the lower to upper portions. Smaller cells of 10-15 μm wide \times 10-12 μm thick are interspersed among these cells. These medullary cells become gradually more slender and shorter toward anticlinal cortical filaments. The cortical filaments are closely packed and consist of thin-walled cells with less frequent secondary pit connections between adjacent cell-rows. The cortical cell-rows are 20-30 at the lowest terete portion, 10-18 at the lower to middle portions and 6-10 at the upper portion. The cortical cells are rectangular and 4-5 μm wide in the outer cortex and 10-15 μm wide in the inner cortex.

Cystocarps are formed on ultimate and penultimate branches; usually in catenate series of 2-7 on long branches of 7-12 mm in length (Fig. 17D, E) and sometimes individually on short branches of 2-3 mm in length (Fig. 17C). They are 600-1000 μm long, 700-1000 μm wide and 500-750 μm thick. The cortex around the cystocarp except both margins is much thicker than adjacent vegetative parts; the thickened parts are composed of 18-24 anticlinal cell-rows and are 140-200 μm thick (the cortex of one side is slightly thicker than that of the opposite side), whereas vegetative parts are composed of 6-8 cell-rows and are 30-40 μm thick. The cystocarpic parts are prominent and 800-1100 μm thick, while the adjacent vegetative parts are 300-400 μm thick. The cystocarpic parts are also broader than the adjacent vegetative parts (Fig. 17C-E) and 900-1500 μm wide. The cystocarp is provided with multiple carpostomes in the thickened cortex. The carpostomes are composed of short periclinal filaments produced from anticlinal filaments and the cavity (Fig. 15G).

The remaining specimens of *G. catenatus* determined by YENDO are different from the lectotype in having broader thalli of 1.2-1.8 mm wide except at the forks, larger medullary cells of 50-100 μm wide and a thinner cortex composed of 4-8 anticlinal cell-rows at the middle to upper portions. They are identifiable with *G. flabelliformis* HARVEY by these features, although these specimens seem not to belong to a single breeding group of that species (MASUDA, unpublished). *G. catenatus* is vegetatively characterized by having a narrow thallus, slender medullary filaments and a thick cortex. The thick cortex is attributed to the perennial growth of thalli. Distinct limiting lines between the layers of the cortex (Fig. 15E) show growth rings.

Gymnogongrus catenatus has been collected at several localities in southern and central Japan other than the type locality: (1) Aoshima, Miyazaki Prefecture, May 25, 1982, leg., T. YOSHIDA and M. MARUI, SAP 048715; (2) Hyuga, Miyazaki Prefecture, April 6, 1985, leg., M. MASUDA, SAP 048714; (3) Nobeoka, Miyazaki Prefecture, May 24, 1982, leg., T. YOSHIDA and M.

MARUI, SAP 048712-3; (4) Ashizurimisaki, Kochi Prefecture, August 28, 1983, leg., K. OKUDA, SAP 048711; (5) Tosa, Kochi Prefecture, September 6, 1983, leg., M. OHNO, SAP 048710; (6) Shingu, Wakayama Prefecture, July 19, 1985, leg., T. YAMAMOTO, SAP 048705, 048709; (7) Iwaizaki, Mie Prefecture, October 26, 1981, leg., T. YOSHIDA and T. KONNO, SAP 048706; (8) Nakiri, Mie Prefecture, February 1923, leg., Y. YAMADA, SAP 048716; and (9) Arashima, Mie Prefecture, March 8, 1984, leg., M. MASUDA, SAP 048707-8.

Supplementary data are given on the basis of living and liquid-preserved specimens collected at Arashima, Toba situated about 4 km to the north-west of Ijika, the type locality. Upright thalli are dark red in color and cartilaginous. The thick cortex and appressed, slender medullary filaments may contribute to its cartilaginous texture. Proliferations develop from scars of branch apices. This suggests that the grazed ends of branches produce proliferations. This phenomenon was frequently observed during phenological investigation of *Gymnogongrus flabelliformis* in Oshoro Bay, Hokkaido (MASUDA and TAKEUCHI, unpublished). Spermatangia are formed in a sorus near the apices of branches and proliferations. One or two spermatangia are

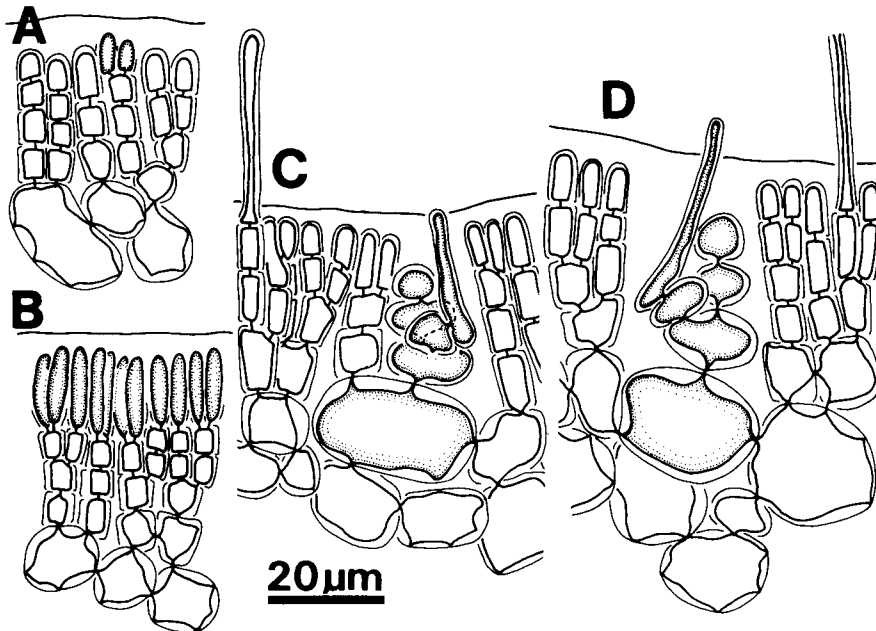


Fig. 16. *Gymnogongrus catenatus*. All from specimens collected at Arashima, Mie Prefecture on March 8, 1984. A, B: Development of spermatangia (longitudinal section). C, D: Development of procarps (longitudinal section); note colorless hairs.

produced from a single spermatangial parent cell (Fig. 16A, B). Mature spermatangia are $13\text{--}17\ \mu\text{m}$ long \times $2.5\text{--}3.0\ \mu\text{m}$ wide. Procarys are formed in groups in the center of apices of branches and proliferations. Procarys are provided with unicellular colorless hairs formed from the outermost cortical cells (Fig. 16C, D). Each procarys consists of a large supporting cell, a three-celled carpogonial branch and a two-celled sterile branch borne on the first cell of the carpogonial branch (Fig. 16C, D). Cystocarys are usually formed in catenate series (Fig. 17B), but they are sometimes produced individually even on long branches or proliferations (Fig. 17A).

OKAMURA (1936) rejected *G. catenatus* as a species. Since then, this species has not been mentioned in the literature. Re-examination of YENDO's specimens and recent collections of the alga, however, reveal that *G.*

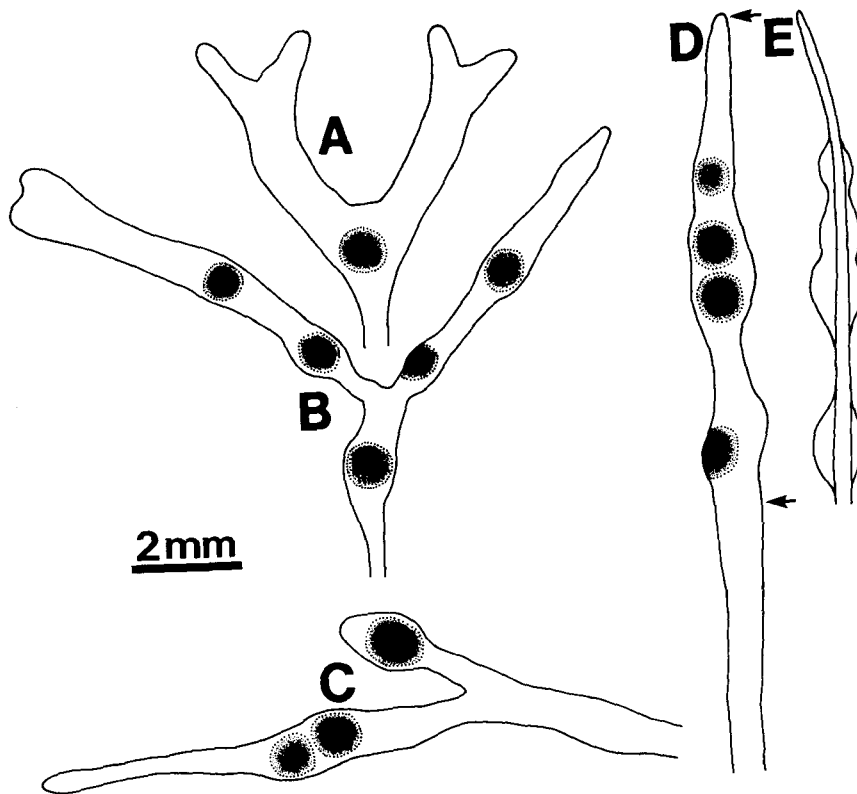


Fig. 17. *Gymnogongrus catenatus*. A, B, from Arashima specimen; C-E, from the lectotype. A, B: Cystocarpic proliferations (surface view). C-E: Cystocarpic branches; C, D, surface view; E, lateral view of the portion between two arrows in D.

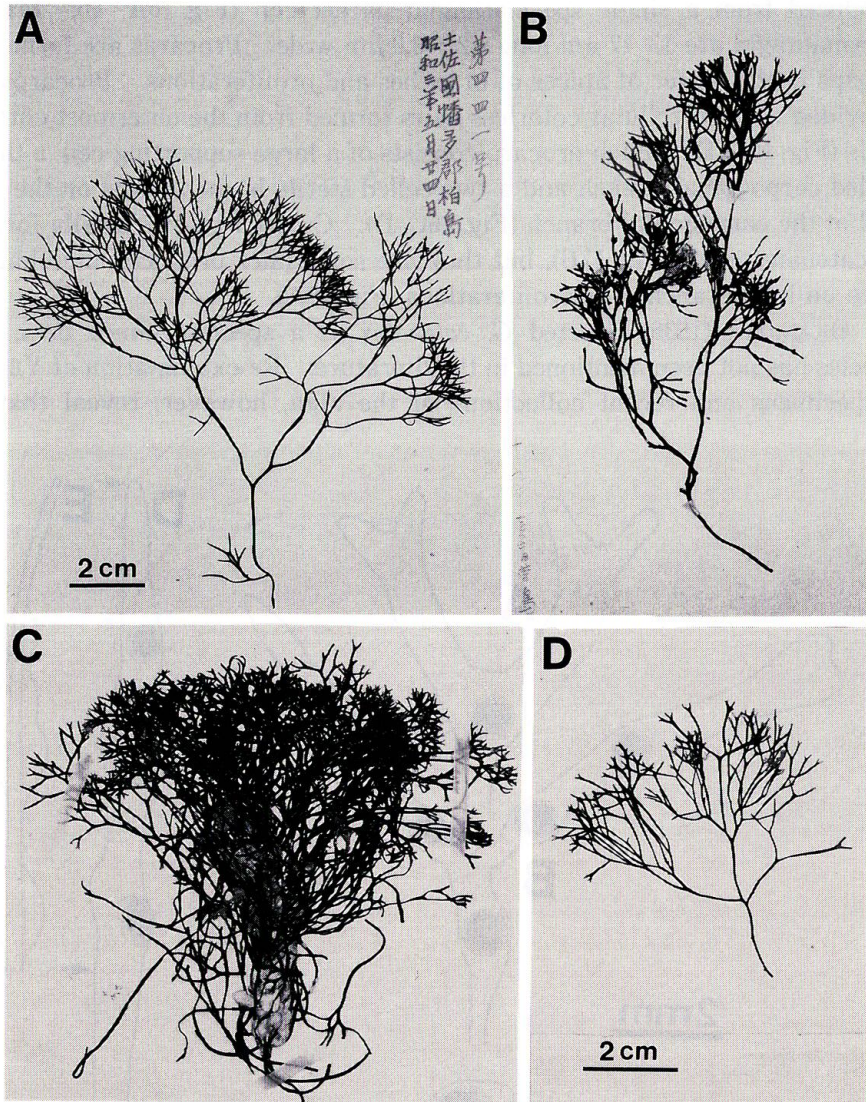


Fig. 18. *Gymnogongrus catenatus*. A: Cystocarpic specimen collected at Kashiwajima, Kochi Prefecture on May 24, 1928 (determined as *Ahnfeltia paradoxa* by Okamura, in his collection in SAP). B: Cystocarpic specimen collected at Sugashima, Mie Prefecture on July 6, 1944 (determined as *Ahnfeltia paradoxa* by Yamada, SAP 048614). C: Spermatangial specimen collected at Uchinoura, Kagoshima Prefecture in August 1940 (determined as *Ahnfeltia paradoxa* by Nakamura, SAP 024130). D: Spermatangial specimen collected at Owase, Mie Prefecture in 1933 (determined as *Gymnogongrus japonicus* by Okamura, in his collection in SAP). Scale in D applies also to B and C.

catenatus is a distinct species. Furthermore, a check of herbarium specimens of *Gymnogongrus* and *Ahnfeltia* species deposited in SAP reveals that *G. catenatus* has been confused with *G. paradoxus* (as *Ahnfeltia paradoxa*) and *G. japonicus* by some previous investigators. OKAMURA (1936) reported *A. paradoxa* from many localities ranging from Kyushu to northern Honshu. His specimens collected at Hosojima, Hyuga, Miyazaki Prefecture; Kashiwajima, Ootsuki, Kochi Prefecture (Fig. 18A); and Tanokuchi, Oogata, Kochi Prefecture are identifiable with *G. catenatus*. These specimens are elongated, but they share the aforementioned features with *G. catenatus*. TAKAMINE and YAMADA (1950) reported *A. paradoxa* from Sugashima, Mie Prefecture. Their voucher specimens (SAP 048614) are nothing but *G. catenatus* (Fig. 18B). MIKAMI (1965) included Uchinoura, Kagoshima Pre-



Fig. 19. Distribution of *Gymnogongrus catenatus*, compiled from specimens in SAP and TI.

fecture within the geographical range of *A. paradoxa* on the basis of a specimen collected by Y. NAKAMURA (SAP 024130) (Fig. 18C). This specimen, however, compares very favorably with *G. catenatus* in every respect. Voucher specimens of OKAMURA's (1936) *G. japonicus* include *G. catenatus*, which was collected at Owase, Mie Prefecture (Fig. 18D).

On the basis of specimens cited in this section the present known range of *G. catenatus* is shown in Fig. 19. This species is distributed along the Pacific coast of Japan ranging from Kagoshima to Mie Prefecture.

Concluding Remarks

Of the six taxa studied, *Gymnogongrus flabelliformis* HARVEY, *G. paradoxus* SURINGAR, *G. divaricatus* HOLMES and *G. catenatus* YENDO can be recognized as distinct taxonomic species. *G. japonicus* SURINGAR and *G. furcellatus* var. *japonicus* HOLMES should be placed in synonymy with *G. flabelliformis* and *G. paradoxus*, respectively. These four species have the following features in common: (1) the upright thallus is compressed (except the lowest terete portion) and dichotomously branched; (2) the structure of medulla is compact and pseudoparenchymatous; (3) in the medulla small cells are interspersed among large cells; (4) proliferations are formed from the margins; (5) the three-celled carpogonial branch always bears a sterile branch composed of one or two cells; (6) the spermatangia are anticlinally elongated; (7) the cortex around inwardly developing cystocarps becomes much thicker than adjacent vegetative parts; and (8) multiple carpostomes for spore discharge are formed in the thickened cortex. Furthermore, the tetrasporangia of these species are formed seriatly in an intercalary position on upright filaments of a nemathecium which is borne on *Erythrodermis*-like crustose plants (MASUDA *et al.*, 1979; MASUDA, 1981, 1982, unpublished).

Taxonomic features characterizing each species are summarized as follows. The branching intervals and angles contribute to the thallus shape. *G. flabelliformis*, *G. divaricatus* and *G. catenatus* have fan-shaped to almost circular thalli according to the short intervals and wide angles. This feature is the most conspicuous for *G. divaricatus*. *G. paradoxus*, however, has a broom-shaped thallus as a result of the long intervals and narrow angles. This species is also characterized by abundant proliferations which fill the intervening space between branches. These proliferations sometimes develop well and show a fan-shaped outline. The detached proliferations themselves resemble *G. flabelliformis* or *G. divaricatus*.

All the species examined are narrowly linear. Though subtle, the thallus width is characteristic. *G. catenatus* possesses the narrowest thallus less

than 1 mm wide, whereas *G. divaricatus* and *G. paradoxus* have thalli ranging from 2 to 3 mm wide. *G. flabelliformis* has a thallus width intermediate between them.

These species are anatomically characterized by the dimensions of medullary cells and the numbers of anticlinal cortical cell-rows. *G. divaricatus* has the broadest medullary cells of 60-170 μm wide, whereas *G. paradoxus* and *G. catenatus* have the narrowest cells of 20-45 μm wide. *G. flabelliformis* possesses medullary cells intermediate size between them. In relation to the dimensions, the numbers of medullary filaments are characteristic. *G. paradoxus* and *G. catenatus* with narrow cells possess some 20 medullary filaments except the lowest terete portion, whereas *G. divaricatus* with the broadest cells have 10 or less filaments. *G. flabelliformis* is again intermediate. *G. paradoxus* and *G. catenatus* produce thick cortices from the lower to middle (or upper) portions, while the other two species do not form such cortices except the lowest terete portion. The difference is due to the perennial growth of the former two species. Narrow and abundant medullary cells and thick cortices may give *G. paradoxus* and *G. catenatus* a cartilaginous texture. *G. catenatus* resembles narrow plants of *G. flabelliformis*, but it is readily distinguishable from the latter by its hard texture in their sympatric field.

These species show close similarity in reproductive structures, but some subtle differences are found in the dimensions of spermatangia, the numbers of sterile cells of carpogonial branches and the numbers of anticlinal cell-rows around cystocarps. *G. paradoxus* and *G. catenatus* produce slightly larger spermatangia than the other two species. *G. paradoxus* has a one-celled sterile branch on the carpogonial branch, whereas the other three species always possess a two-celled sterile branch. *G. catenatus* has the thickest cortex around the cystocarp which consists of 18-24 anticlinal cell-rows about twice those of the others.

The above-mentioned features are based on the type specimens and specimens collected chiefly from the type localities of these species. The taxonomic significance of the features must be verified on the basis of specimens from their whole geographical ranges. Such a study is in progress.

The similarity of reproductive features in the species examined shows their close affinity in this genus. These species form a group in *Gymnogongrus* together with some foreign species, *G. furcellatus* (C. AGARDH) J. AGARDH (CANDIA and KIM, 1977), *G. leptophyllus* J. AGARDH (DECEW and WEST, 1981), *G. linearis* (C. AGARDH) J. AGARDH (DECEW and WEST, 1981)

and *G. crustiforme* Dawson (WEST, DECEW and MASUDA, unpublished). Another group is characterized by having external pustule-like tetrasporoblasts. This group includes *G. griffithsiae* (TURNER) MARTIUS, the type species of the genus (GREGORY, 1934; SCHOTTER, 1968; CORDEIRO-MARINO and POZA, 1981), *G. crenulatus* (TURNER) J. AGARDH (SCHOTTER, 1968 as *G. norvegicus*; ARDRÉ, 1978) and *G. chiton* (HOWE) SILVA et DECEW (DOUBT, 1935 as *G. platyphyllus*). These investigators, except CORDEIRO-MARINO and POZA (1981), reported that gonimoblasts (=tetrasporoblasts, or nematocial filaments) initially develop inwardly and later protrude outwardly without the formation of carposporangia. According to CORDEIRO-MARINO and POZA (1981), however, the Brazilian *G. griffithsiae* produces an internal cystocarp forming carposporangia and carpospores germinate within the gametophyte. The alga shows an intermediate stage between the first and second groups of *Gymnogongrus*. The taxonomic relationship between the two groups requires further consideration. This question is entangled with the taxonomic status of several species still placed in *Ahnfeltia*.

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