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On the systematic position of the parasitic red alga *Kintokiocolax aggregatocerantha* TANAKA et Y. NOZAWA

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Reproductive morphology of *Kintokiocolax aggregatocerantha* TANAKA et Y. NOZAWA, a parasitic red alga on the host *Prionitis angusta* (=*Carpopeltis angusta*), was studied in detail based on the specimens collected at Wakayama and Chiba Prefectures. In these specimens, the auxiliary cell and the 2-celled carpogonial branch were separately produced (non-procarpic) in the secondarily developed cell clusters (ampullary structures characteristic of the Halymeniaceae), and after fertilization the connecting filament was necessary for activating the auxiliary cell to produce gonimoblasts. This result is different from that described by the original authors who interpreted the reproductive structure as procarpic and therefore this species as a member of the Gigartinales.

To clarify this difference in the interpretation of the reproductive structure, we examined the original materials and found that they possessed the same reproductive features as our materials. Thus, we concluded that this species should be placed in the Halymeniaceae (=Cryptonemiaceae).

Key Index Words: *Aadelphoparasite*; *alloparasite*; *Cryptonemiales*; *Halymeniaceae*; Kintokiocolax aggregatocerantha; *parasitic red alga*; *reproductive morphology*; *Rhodophyceae*.

Kintokiocolax aggregatocerantha TANAKA et Y. NOZAWA (1960) was described as a parasite on the *Prionitis angusta* (HARVEY) OKAMURA (=*Carpopeltis angusta*)* based on the specimens collected at Hananose, Kagoshima Prefecture, Southern Kyushu. They placed this monotypic genus in the order Gigartinales (sensu SCHMITZ in ENGLER) on account of their interpretation that this species has procarpic nature. Since then, as far as is known, no investigation has been published on this species except for a short comment by FELDMANN and FELDMANN (1963).

Recently, small, whitish, seemingly parasitic plants were found on the specimens of *P. angusta* collected at the two localities in the central Pacific coast of Honshu. Gross morphological and inner vegetative features of these specimens were in good accordance with those of *K. aggregatocerantha*, while the reproductive structures were clearly different from those interpreted by TANAKA and NOZAWA (1960). A careful comparison of our specimens with the Holotype and the Isotype of *K. aggregatocerantha* revealed that both of the type specimens had the same reproductive features as ours. We noticed that the reproductive structures of this species were characteristic of the Halymeniaceae, Cryptonemiales.

* In the original description, the binominal *Carpopeltis angusta* (HARVEY) OKAMURA was used, but according to the recent study by KAWAGUCHI (unpubl.), it is most appropriate to treat this species under the genus *Prionitis* as did ABBOTT and HOLLENBERG (1976, p. 444).

Materials and Methods

The materials used for the present study were:

1) Hananose, Kagoshima Prefecture, 10 June, 1959, collected by T. TANAKA & Y. NOZAWA (Holotype and Isotype deposited in the herbarium of Faculty of Fisheries, Kagoshima University).
2) Hikigawa, ca. 15 m deep, Wakayama Pref., 26 Nov., 1984, collected by T. YOSHIDA (SAP 047798).
3) Ohara, 25–32 m deep, Chiba Pref., 27 Aug., 1985, collected by M. OHTA (SAP 047801).

The materials used for anatomical study were preserved in formalin-seawater except for the type materials. Sections were made by hand using a razor blade and stained with cotton blue solution. They were mounted in 50% glycerol-seawater on microscope slides.

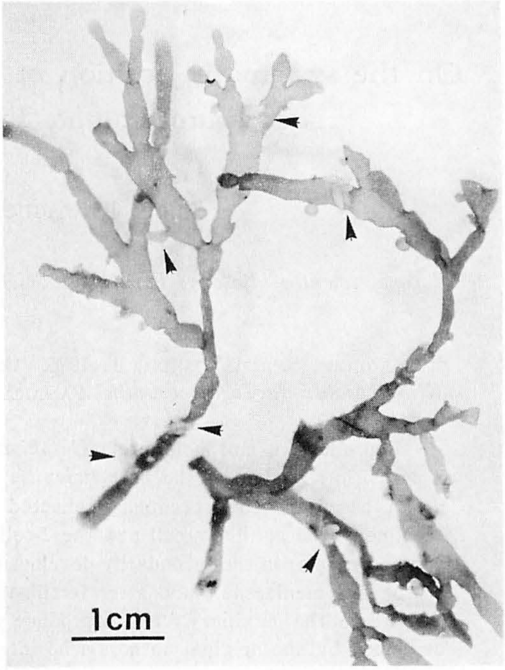


Fig. 1. *Kintokiocolax aggregatocerantha* TANAKA et Y. NOZAWA. Habit of parasitic plants (arrowheads) scattered over the host *Prionitis angusta* (HARVEY) OKAMURA collected at Hikigawa.

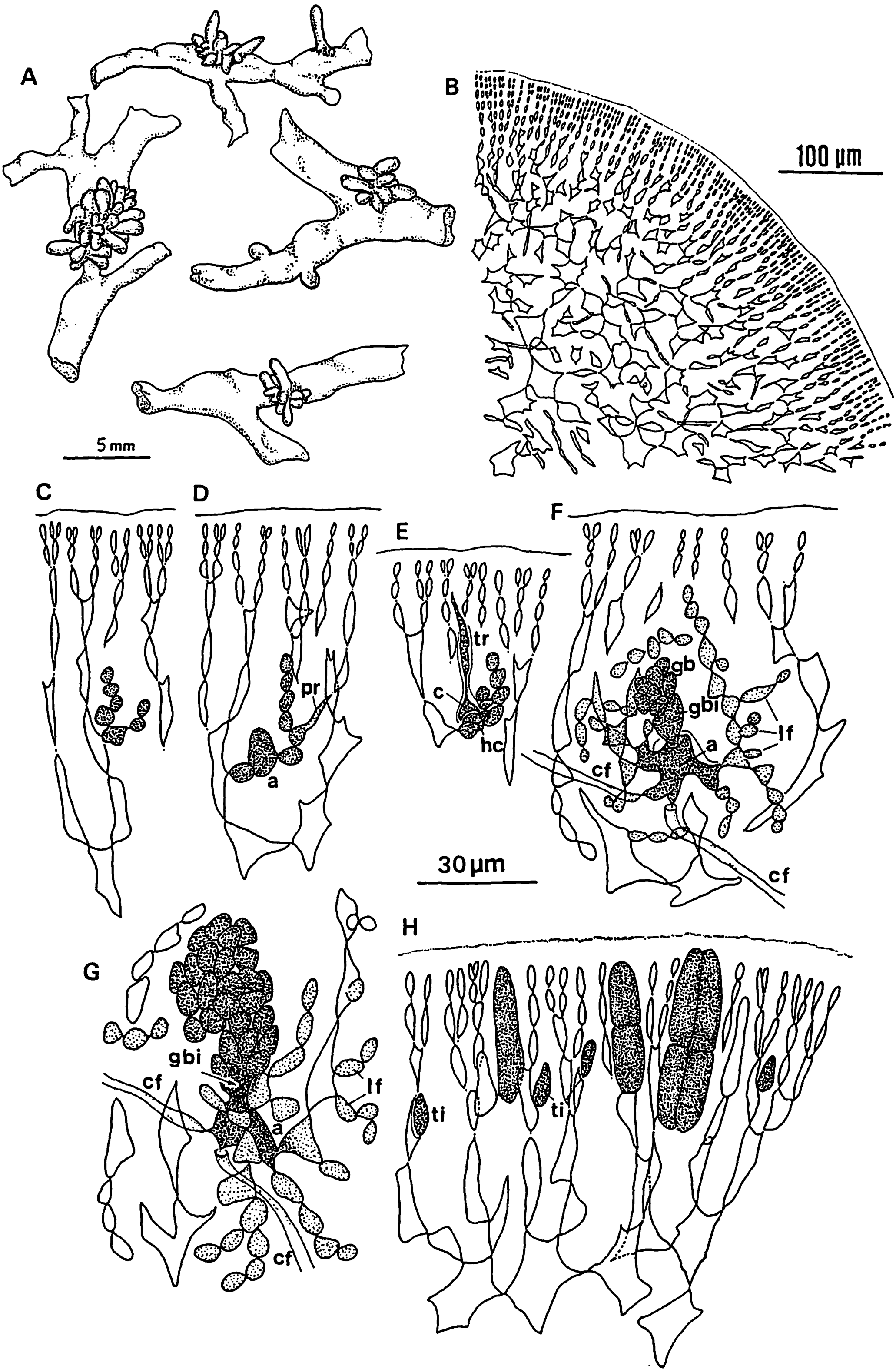
Observations

The following observations are based on the specimens collected at Hikigawa and Ohara.

Habit: Plants are found scattered over the host thallus, forming small, irregular-shaped wart-like masses (Fig. 1, arrowheads). Each plant consists of a basal cushion-like part, up to 5 mm in diameter, and short erect columnar shoots. The erect shoots, one to twenty in number, develop from the basal part, up to 5 mm high and 1 mm in diameter, and the apex of a shoot is blunt or sometimes pointed (Fig. 2A). They are somewhat cartilaginous in texture, with rather smooth surface. The color is usually yellowish white or at times pale pink.

Vegetative structures: In longitudinal section through the host thallus, the parasite seems to attach to the host by its flattened layer, showing no connections with the host in some areas (Fig. 3A). While in other areas of the same plant, the parasite tissue can hardly be distinguishable from the host tissue and seems to be continuous with the outer cortical cells of the host. In the latter case, however, we could not determine whether connections between the host

Fig. 2. *Kintokiocolax aggregatocerantha* (Hikigawa specimens). A. Habit of parasitic plants on hosts. B. Cross section of erect shoot. C. Young branch system secondarily produced from inner cortical cell. D. Auxiliary cell (a) branch system composed of a single filament. Note that a lateral protuberance (pr) develops from a cell in the branch system. E. Carpogonial branch system bearing carpogonium (c) and hypogynous cell (hc). F. Young stage in gonimoblast development. Lateral filaments (lf) produced from cells in the branch system. G. Advanced stage in gonimoblast development. Pit-connection between auxiliary cell (a) and gonimoblast initial cell (gbi) becoming wide. Lateral filaments (lf) produced from neighboring vegetative cells. H. Tetrasporangial formation. Tetrasporangial initials (ti) cut off from cortical cells as a single side branch.


A
B
100 µm
5 mm
C
D
E
F
tr
c
hc
pr
a
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gbi
lf
cf
30 µm
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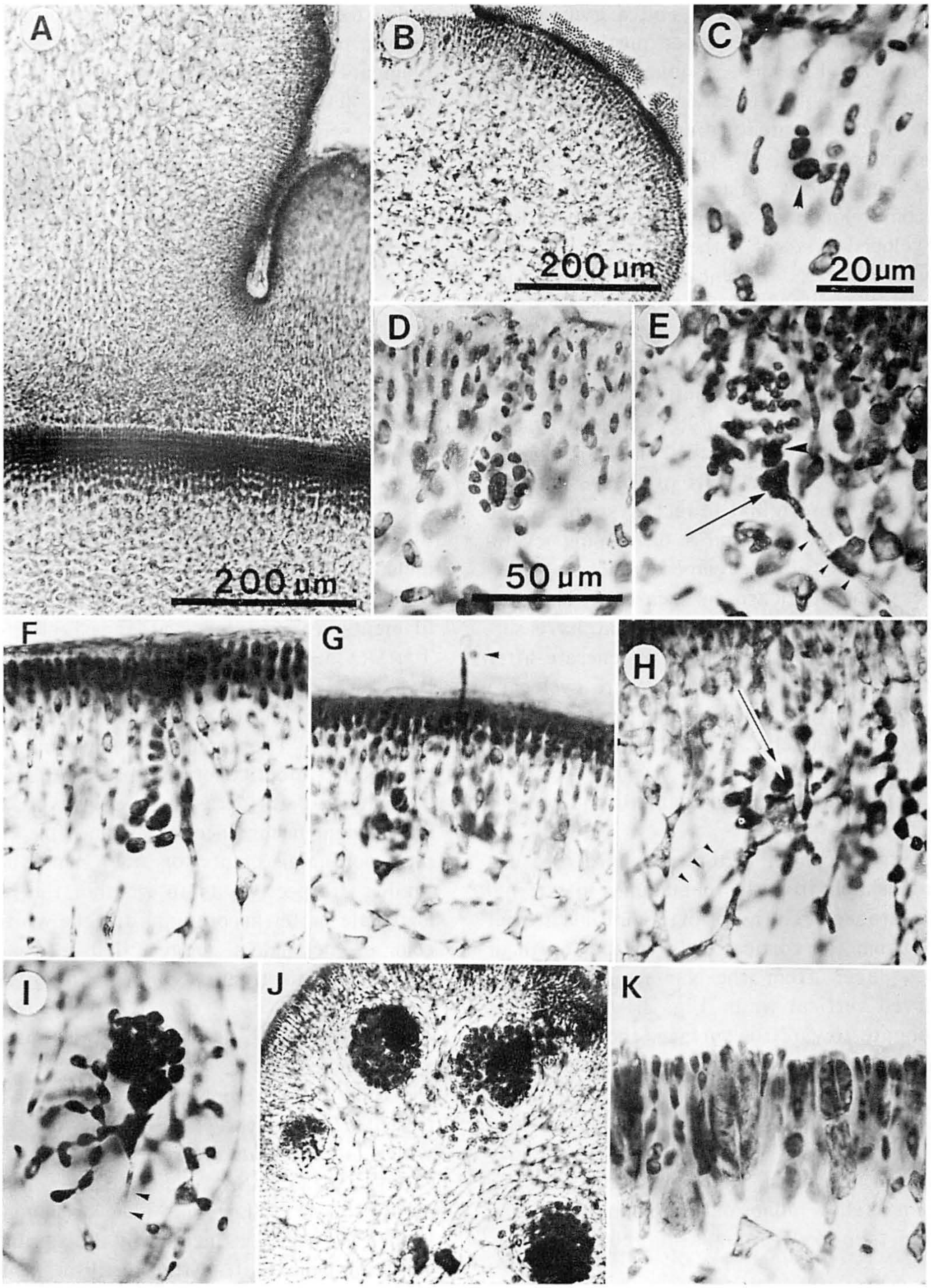
ti

and the parasite were established or not with certainty. No rhizoidal filaments were detected, although many sections were inspected. The erect shoot consists of cortical and medullary layers. The outer cortex is composed of regularly dichotomously branched filaments of small ellipsoid cells (5-8 μm long×3-4 μm broad), about five cells long, laterally free from one another. This outer layer grades to an inner cortex three to five layers deep composed of larger ellipsoid or polygonal cells (8-15 μm×5-8 μm) frequently connected to adjacent cells by secondary pit connections, and in turn grading into a medullary region of irregular-shaped cells also secondarily connected with one another. The cells in the medulla, some of which are very large, reaching 90 μm in diameter, are interconnected by occasional filamentous cells (Fig. 2B). Most of the cells in the cortex and the medulla are almost colorless except for those in the outermost two or three cortical layers. The presence of red pigmentation in the latter cells may show that they play an assimilatory role to a certain degree, although no evidence is available to us.

Reproductive structures: In the specimens at hand, both cystocarpic and tetrasporangial plants were independently found on the same host thallus. The auxiliary cell and the carpogonial branch are formed in the separate branch systems which are secondarily developed laterally from the inner cortical cells (Fig. 2C, D, E). These branch systems are identical to the structures called ampullae of the Halymeniaceae. The carpogonial branch is two-celled, consisting of a carpogonium and a hypogynous cell (Fig. 2E). The hypogynous cell seems to be intercalarily situated because it has a single side branch (Fig. 2E). The carpogonium, usually conical in shape, projects a trichogyne from the upper portion toward the thallus surface. The branch system bearing an auxiliary cell is basically the same in structure as that bearing the carpogonial branch, and consists of a few filaments branched at most to the second order (Fig. 3F). As shown in Fig. 2D, the auxiliary cell branch system is often composed of only a single filament. The auxiliary cell is intercalary, usually the second cell of the primary filament, or the first cell of the second order filament issued from the first cell of the primary one (Fig. 2D). In some cases, the first cell of the primary filament functions as an auxiliary cell. The auxiliary cell is easily distinguished from other cells in the branch system by its larger size and denser protoplasmic content.

The early stage of post-fertilization development was not clarified (a supposed spermatium attaching close to the top of a trichogyne was found only in one case (Fig. 3G)), but the connecting filaments were clearly observed attached to auxiliary cells (Figs. 2F, G; 3I). The connecting filament may cease to grow when the contact with an auxiliary cell has been established, but in many cases a new connecting filament is cut off from other side of the auxiliary cell. After receiving fertilized nucleus through

Fig. 3. *Kintokiocolax aggregatoceranthа* (A and F-K: Hikigawa specimens; B-E: Holotype and Isotype). A. Longitudinal section of the plant (above) through its host (below) showing that it attaches to the host by its flattened layer. B. Cross section of female shoot. C. Young branch system bearing auxiliary cell (arrowhead). D. Auxiliary cell branch system. E. Young stage in gonimoblast development. Gonimoblast initial cell (large arrowhead) cut off from auxiliary cell (arrow) after contact with connecting filament (small arrowheads). F. Sparsely branched auxiliary cell system. G. Supposed spermatium (arrowhead) attached to a trichogyne projected from the surface. Note that the branch system below is out of focus. H. Early stage in gonimoblast development showing that gonimoblast initial cell (arrow) has just been cut off from auxiliary cell after contact with connecting filament (arrowheads). I. Young stage in gonimoblast development. Connecting filament (arrowheads) attached to auxiliary cell. J. Cross section of erect shoot showing mature cystocarps embedded in the interior of the thallus. K. Tetrasporangia embedded in cortex. Scale bar in B applies also to J, and D to E-I and K.


A
B
C
200 μm
20μm
D
E
200 μm
50 μm
F
G
H
I
J
K

the connecting filament, the auxiliary cell slightly enlarges and cuts off a gonimoblast initial cell from the upper portion by concave wall (Fig. 3H). Gonimoblast cells are successively developed from the initial cell and they repeatedly divide to form carposporangia (Figs. 2F, G; 3I). Some cells of the gonimoblast adjacent to the initial cell become elongated and remain sterile. In a developed cystocarp, the gonimoblast initial cell is elongated to some degree and becomes difficult to discriminate from the auxiliary cell lying beneath it (Fig. 2G).

Concurrently with the gonimoblast development, the neighboring vegetative cells together with those of the branch system produce simple or branched lateral filaments (Fig. 2F, G). The cells of these filaments and also the original branch system become elongated to surround a developing cystocarp. In a fully developed cystocarp, however, the pericarp is scarcely observed probably because those cells that have surrounded a young cystocarp degenerate after supplying nutrition. The mature cystocarp is spherical to hemispherical in shape, 150–180 μm in diameter, embedded in the interior of a thallus (Fig. 3J).

Male plants were not found in the present study.

Tetrasporangial plants can hardly be distinguishable from the female ones in external appearance. Tetrasporangial initials are cut off from the cortical cells in the fourth or fifth layer from the surface by slightly curved vertical walls (Fig. 2H). They first elongate toward the surface, then enlarging into narrowly ellipsoid sporangia. The mature sporangium is 37-40(-45)$\times$10-15 μm in size, cruciately or decussately divided (Figs. 2H; 3K). In some plants, irregularly divided sporangia were abundant, and they seem to show abnormal development judging from their poor protoplasmic contents.

Observations on the type materials

The habit and the vegetative structures of the Holotype and the Isotype were the same as the original description by TANAKA and NOZAWA (1960). The only different feature obtained by us is that no rhizoidal filaments were observed in the sections we made. The parasite attaches to the host in the same way as described earlier on the specimens from Hikigawa and Ohara.

The reproductive structures of the type specimens obviously differed from those interpreted by TANAKA and NOZAWA in that the auxiliary cell and the carpogonial branch were separately formed in the secondarily developed ampullary cell clusters (Fig. 3D), and that the connecting filament was necessary for activating the auxiliary cell to produce gonimoblasts (Fig. 3E).

Discussion

As far as the materials examined by us, including the Holotype and the Isotype, are concerned, we could not find any rhizoidal filaments as was reported and figured by TANAKA and NOZAWA (1960, p. 110, fig. 4A, B). According to our observations, the plant appears to attach to the host by its flat surface. There remains some doubt on the distinct identity of the present alga or the nature of its parasitism. However, the independent occurrence of cystocarpic and tetrasporangial plants on the same host thallus irrespective as to whether the host is female or tetrasporangial and the whitish color of the thallus suggest that it is most appropriate to treat *K. aggregatocerantha* as a parasite.

In the original description, this species was considered to belong to the Gigartinales and thus to represent an example of alloparasite (FELDMANN & FELDMANN, 1958), which is minor in the red algal parasites (GOFF, 1982). TANAKA and NOZAWA (1960) described as follows: "The carpogonial branch is directly connected by the auxiliary cell lying beneath it. After fertilization, the auxiliary cell produces another two or three nourishing cell groups and forms a large fusion-cell which brings forth the gonimoblast." Their fig. 3B, C (p. 108), however, does not give any exact image on the post-fertilization events. FELDMANN and FELDMANN (1963, p. 558-559) stated that " A en juger par les figures publiées, cette attribution du genre *Kintokiocolax* aux Gigartinales ne nous parait pas justifiée ", on the grounds that the disposition of the differentiated short filaments is not that of the Gigartinales but shows the structure very similar to the carpogonial ampulla characteristic of the Halymeniaceae. As is clear from our observations, the above suggestion by FELDMANN and FELDMANN proves to be true. The auxiliary cell and the carpogonial branch are separately formed in the " subsidiary " (KRAFT and ROBINS, 1985) ampullary branch systems. This clearly shows that this species is non-procarpic and has the reproductive features possessed by the members of the Halymeniaceae. The process of gonimoblast development also quite agrees with those hitherto reported in many species of the family (cf. BALAKRISHNAN, 1961, 1961a; KAWABATA, 1962, 1963; CHIANG, 1970). This species is an adelphoparasite as are most of the red algal parasites (FELDMANN and FELDMANN, 1958; GOFF, 1982).

In separating the genera of the family Halymeniaceae, the auxiliary cell structure is considered to be of value by CHIANG (1970). According to him, the auxiliary cell ampullary structures can be divided into 5 types in the family from the shape and the degree of branching, and sparsely-branched ampulla is more advanced than densely-branched one. If based on his system, the auxiliary cell ampulla of this species clearly falls within the range of advanced category, or is rather more advanced than any type because it is often composed of only a single filament as shown in Fig. 2D. This reduced type of ampulla has never been reported in the members of this family nor has been observed in the host species *P. angusta* (KAWAGUCHI, unpubl.). It might be possible to say that such a reduction of ampullary filaments represented by this species is due to its parasitism.

Until our present investigation, this species escaped from the attention of other workers. The reason probably lies in its rare occurrence, but also in the fact that it is only found on the *Prionitis angusta* collected from deeper places as is known from the collection data. Diligent search in the subtidal zone might bring more specimens suitable for further investigation.

Acknowledgements

We wish to express our cordial thanks to Prof. Emeritus M. KUROGI, Hokkaido University, for his kind guidance and to Dr. M. MASUDA, Hokkaido University, for his valuable suggestions during the course of our present study. Special thanks are due to Dr. M. OHTA, Central Laboratory, Marine Ecology Research Institute, who contributed the specimens at our disposal. We are also grateful to Prof. K. NOZAWA, Kagoshima University, for the loan of the type specimens.

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川口栄男・吉田忠生：寄生紅藻キントキヤドリ *Kintokiocolax aggregatocerantha* TANAKA et Y. NAZAWA の分類学的位置

キントキ *Prionitis angusta* (=*Carpopeltis augusta*) 上の寄生紅藻として知られる本種は，助細胞と造果枝が直接連結する (procarpic) という原著者らの解釈に基づき，スギノリ目 Gigartinales の種として発表された。しかし，和歌山県と千葉県で新たに採集された材料を詳しく調べた所，その雌性生殖器官の構造には，原報告と明らかに異なる点が見い出された。すなわち，助細胞と造果枝は離れて，それぞれ別の二次的に形成された枝叢中に存在した (non-procarpic)。

この違いを基準標本について検討した結果，著者らの観察事実と一致した特徴を有することが確認された。従って，本種はカクレイト目 Cryptonemiales ムカデノリ科 Halymeniaceae に属するとの結論に達した。(060 札幌市北区北10条西8丁目　北海道大学理学部植物学教室)

新　刊　紹　介

R. F. SCAGEL, D. J. GARBARY, L. GOLDEN & M. W. HAWKES (1986) **A Synopsis of the Benthic Marine Algae of British Columbia, Northern Washington and Southeast Alaska.** Phycological Contribution No. 1, The University of British Columbia, Vancouver, Canada. 444 pp. 22.5 カナダ$ (含船郵送料，邦貨約 2,800 円)

本書はカナダの太平洋沿岸における初めての本格的な海藻のチェックリストである SCAGEL, R. F. (1957) “An annotated list of the marine algae of British Columbia and northern Washington” の続編である。1957年以降にこの海域から報告されている海藻の採集記録のほとんどすべてを網羅している。前書に収録されている 189 属 478 種をはるかに上回る 270 属 627 分類群が収録されている。その内訳は黄緑色藻類 3 属 6 分類群，緑藻類45属 102 分類群，褐藻類66属 130 分類群，紅藻類 156 属 389 分類群となっている。

本書は大きく 2 つの部分に分けられる。前半は各分類群の採集報告が 180 頁にわたって記載されており，後半に約2000点の文献のリストが 146 頁にわたって載せられている。前半部の分類群名の後には，著者名や出典は勿論のこと Basionym やカナダ以外での世界各地の分布も書かれてあり，海藻の名前調べや分布調べにとても便利である。言うまでもなく分類群の索引としても第1級の精度を持っている。しかしここまで述べてきた内容を持っているものは本書以外にもかなりある。本書のもっとも大きな特色は，収録されている文献の種類が分類学だけでなく，遺伝学，形態学，分布地理学，生化学，生理学，生態学など多方面にわたっていることである。様々な分野の研究材料として採集された記録をのこらず載せてあるので，本書は海藻を材料として用いる研究者にとって大いに役にたつ書であると確信できる。最近数多く出版される海藻フロラや海藻チェックリストのなかで本書はその白眉と言えるものである。入用の方は，R. F. SCAGEL, Dept. Bot., Univ. of British Columbia #3259-6270 University Blvd., Vancouver, B. C. V6T 2BI, Canada へ直接申し込むこと。(国立科学博物館植物研究部 田中次郎)