Nuclear SSU and Plastid *rbc*L Genes and Ultrastructure of *Mallomonas caudata* (Synurophyceae) from Korea

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Despite geographic barriers such as oceans, many freshwater algal species inhabit different continents of the world. A unicellular freshwater alga, Mallomonas caudata, commonly occurring in Asia, Europe, and America of the northern Hemisphere, is closely related to human life such as monitoring blooms and detecting changes in climates. In order to demonstrate its occurrence in Korea and to infer its phylogeny, we sequenced nuclear SSU and plastid rbcL genes from isolates collected in six different reservoirs. We have also investigated transmission electron microscopy of the Korean isolates. SSU sequences of the species from Korea and USA were almost identical, having pair-wise divergences of 0.06% in SSU and 0.45% in rbcL. Both gene trees revealed that the species was clearly separated from other species of the genus, while the genus was not monophyletic. Rhizoplasts are composed of microfibrils organised in striated rootlets attached to the multilayered plate of basal bodies and arranged on the surface of the nucleus at their distal ends. The rhizoplast constitutes a basal body-nucleus connector similar to that of typical Synurophyceae. The results that Mallomonas was not supported by both SSU and rbcL data sets require a further study with additional taxon sampling.

Key words : $Mallomonas\ caudata$, phylogeny, rbcL, SSU rDNA, stramenopiles, rhizoplast, ultrastructure

INTRODUCTION

Mallomonas Perty is a unicellular freshwater genus with approximately 183 species that occurs commonly worldwide (Rezacova and Neustupa, 2007). The genus is an important component of biomass as well as contributes species diversity of the phytoplankton community in the lakes and water reservoirs (Kristiansen, 1975; Takahashi, 1978). Some species of the genus form very dense blooms (Kristiansen, 1971; Hoffmann and Wille, 1992; Kim and Hwang, 2001), which negatively affected tastes and odour of potable water (Clasen and Bernhardt, 1982). The genus is characterized

by unicellular system and an amour of silica scales and bristles with one to two bilobed chloroplasts, and two parallel flagella, one of which is much reduced in the majority of species (Siver, 1991; Wee, 1997). The siliceous cell covering consists of individual plates known as scales that are imbricated and arranged in a very precise manner (Takahashi, 1978; Asmund and Kristiansen, 1986; Siver and Glew, 1990). Classification of *Mallomonas* is exclusively based on the morphology and scanning electron microscopy of siliceous scales and bristles (Kristiansen, 1979; Wee, 1982; Asmund and Kristiansen, 1986). However, there are difficulties in their identification because some species showed a transitional scale

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structure in natural samples and scales in a single clonal culture sometimes varied according to cultured conditions (Siver, 1987; Martin-Wagenmann and Gutowski, 1995; Lee and Kim, 2007). To date, approximately 32 species of *Mallomonas* are reported to occur in Korea (Kristiansen *et al.*, 1990; Kim, 1995, 1997; Kim *et al.*, 1995), but little is known on molecular systematics of the species.

Mallomonas caudata Ivanoff is the most common and widespread species in the family Synurophyceae (Asmund and Kristiansen, 1986; Siver, 1991). It is an ovoid to spindle shaped and small alga, usually not exceeding 60 µm in length and 25 µm in width, covered with distinctive scales and bristles (Takahashi, 1978; Siver, 1991; Kim, 1997). It was first reported in Russia (Ivanoff. 1899), followed by northern Europe (Asmund and Kristiansen, 1986) and north America (Wujek, 1978). The species also occurs in Korea (Kim, 1997; Kristiansen et al., 1990), Japan (Takahashi, 1978), and China (Hu and Wei, 2006). The species sometimes predominates almost all over the year or its populations show an abrupt maximum and decline in summer in a metalimnetic water (Hoffman and Wille, 1992). The ultrastructure of the species from Kansas, USA was investigated by Wujek (1978). However, despite its common occurrence in the northern Hemisphere and its ecological importance in freshwater algal community, classification and phylogeny of M. caudata is still least attended.

In order to identify the species and deciphering its phylogenetic relationships, nuclear ribosomal SSU and plastid rbcL sequences from six samples collected in Korea were analyzed here. Although both genes are commonly used markers in systematic of algae, there is a SSU data from a single strain of M. caudata (Lavau $et\ al.$, 1997). We also investigated transmission electron microscopy (TEM) of the isolates of the species from Korea, in addition to previous study on the iso-

lates from Kansas, USA, by Wujek (1978). The present endeavor provides basic information on *Mallomonas caudata* in order to use it as a model species for understanding evolutionary biology because of its common occurrence in the world's most aquatic freshwater bodies and its relatively large size within the Synurophyceae.

MATERIALS AND METHODS

Sampling and growth of cells

The six strains of *Mallomonas caudata* were isolated from six different reservoirs in Korea during April to November, 2004. Details of the collection sites and environmental conditions are provided in Table 1. All the isolates were grown in DY III medium (Lehman, 1976) buffered to pH 7. The unialgal culture was maintained at 15 ± 1 °C with illumination of 100 µmol m⁻² s⁻¹ of cool white fluorescent light at a 14:10 h light-dark cycle.

DNA extraction and sequencing

Live cells in a culture tube of each strain were used for DNA extraction. Extraction buffer was added directly into tubes of live cells and following procedures were as described, according to the manufacturer's protocols, in the Qiagen Plant mini kit (Qiagen GmbH, Hilden, Germany).

Polymerase chain reaction (PCR) amplifications of nuclear ribosomal DNA small subunit (SSU) and plastid rbcL were performed with a thermocycler (BioRad, California, USA) and a TaKaRa ExTaq reaction kit (Takara Shuzo, Shiga, Japan). Primers for PCR and DNA sequencing were SR1, SR4, SR9, and SR12 for SSU (Nakayama *et al.*, 1996) and NDrbcL2 and NDrbcL9 for rbcL (Daugbjerg and Andersen, 1997).

A total reaction mixture (25 μ L) consisted of extracted DNA 2 μ L containing 0.5 ~ 1.0 μ g DNA,

Table 1. List and collection information of samples used in the present study.

Strain (code)	pН	$\begin{array}{c} Temperature \\ (^{\circ}C) \end{array}$	EC (μS cm ⁻¹)	Sampling date	Isolation site
$\it M.~caudata~(JCMC)$	7.2	13.8	117.4	Sep-02	Jinchon Swamp (128° 26′N, 35° 43′E)
M. caudata (GSC)	8.0	20.3	76.3	Sep-03	Gongsan-dam (128° 39'E, 35° 56'N)
M. caudata (GCMC)	8.0	20.3	76.3	Sep-03	Kachang-dam (128° 37′E, 35° 48′N)
M. caudata (DGC)	7.8	13.9	218.0	Apr-04	Daegok Reservoir (128° 39'N, 35° 57'E)
M. caudata (AKC)	7.0	11.1	97.5	Nov-04	Angae Reservoir (129° 28′N, 36° 00′E)
M. caudata (MYC)	6.6	16.0	39.0	Nov-04	Miryang-dam (128° 57′N, 35° 28′E)

10X ExTaq buffer (Mg²⁺ free) 2.5 µL, MgCl₂ (25 mM) 1.5 μL, dNTPs 2.0 μL, and Tag polymerase 0.1 µL (Takara ExTaq). The thermal profile for PCR amplification included: 95°C for 4 min for initial denaturation, followed by 34 cycles at 95 $^{\circ}$ C for 1 min; $50 \sim 48 ^{\circ}$ C for 1 min, $72 ^{\circ}$ C for 2 min. The amplification was terminated with a final extension at 72°C for 6 min. PCR products were purified using High PureTM PCR Product Purification Kit (Roche Diagnostics GmbH, Mannheim. Germany) according to the manufacturer's protocols. Cycle sequencing reactions were performed using ABI Prism BigDye Terminator Cycle Sequencing ready Reaction Kit (PE Applied Biosystems, Foster City, CA, USA) and analyzed on an ABI PRISMTM 377 DNA Sequencer (Applied Biosystems, Foster City, CA, USA) at the Center for Research Facilities, Chungnam National University, Daejeon, Korea. Sequences were assembled and edited using Sequence Navigator version 1.0.1 (Applied Biosystems, Foster City, CA, USA). All the gene sequence data analyzed here are lodged with GenBank under the Accession Numbers EF469638-EF469643 for SSU and EF469644-EF469649 for rbcL.

The complete alignments of 25 strains for SSU and 21 taxa for rbcL were collated with the multiple sequences editing program, SeqPup. Multiple alignments were done with selected GenBank sequences. The sequences with ambiguities were coded as missing data. There were no gaps found in all four alignments. Maximum likelihood (ML) analyses of the SSU and rbcL data were performed using PAUP* and a best-fitting evolution model. The model of sequence evolution was chosen based on results from the successive approximation method. Tree likelihoods were estimated using a heuristic search with 100 random-addition-sequence replicates, and TBR branch swapping. To test the stability of nodes, maximum likelihood and parsimony bootstrap analyses were performed with 500 replicates.

Maximum parsimony (MP) analyses were conducted using PAUP*. All heuristic searches were performed with 1,000 replicates, employed the random-addition of sequences, retained only the best tree, held 10 trees at each step, used TBR branch swapping, collapsed zero-length branches, and used MULTREES. Bootstrap support values were calculated using 1,000 replicates with the following options selected: heuristic search; TBR branch swapping; collapse of zero-length branch-

es; and random-sequence-addition with one repli-

Ultrastructure under transmission electron microscopy

Live cells were observed under a light microscope (Nikon Eclipse 80i, Nikon Co., Japan) equipped with differential interference contrast (DIC) optics. Images were saved on hard drive of a computer with DS-5M (Nikon Co., Japan) photomicrographic system attached to the microscope.

For the TEM, cells were fixed in 2.5% glutaraldehde in culture medium for 1.5 to 2 h. Then, cells were centrifuged, and the pellet was agarized. After several medium rinses, the cells were postfixed in 1% osmium tetroxide with deionized water. Dehydration was accomplished using a graded ethanol series (50%, 60%, 70%, 80%, 90%, and 100% ethanol, followed by two 100% ethanol steps). The material was embedded in Spurr's low-viscosity resin (Spurr 1969). Sections were obtained with a RMC MT-XL ultramicrotome (Boeckeler Instruments Inc., USA) and poststained with 3% aqueous uranyl acetate followed by lead citrate. Stained sections were observed under a JEOL-1010 electron microscope (Jeol Ltd., Japan).

RESULTS

Molecular phylogeny

The SSU sequences determined in the present study were of 1821 nucleotides for *Mallomonas caudata* and its putative relatives. The 25 aligned SSU sequences had 98 variable sites (5.4%) and 160 parsimoniously informative sites (8.8%). Within the species, samples from Korea and USA differed by up to 5 bp (0.3% pairwise divergence). However, samples collected within Korea differed by one bp (0.06% pairwise divergence). *M. caudata* and its close relative, *M. matvienkoae*, differed by up to 20 bp (1.2% pairwise divergence). In the phylogenetic tree of the SSU data, all six samples of *M. caudata* produced a strongly supported clade. However, the genus was not monophyletic (Fig. 1).

The *rbc*L sequences determined in the present study were of 1080 nucleotides for *Mallomonas* caudata and its putative relatives. The 21 aligned *rbc*L sequences had 73 variable sites (6.7%)

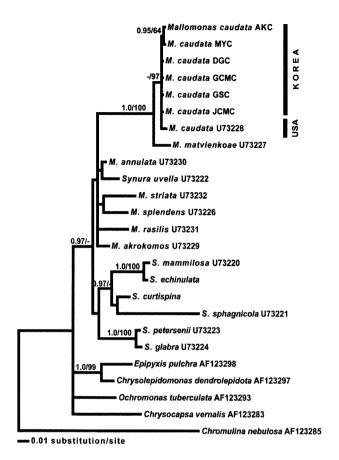


Fig. 1. ML tree of nuclear SSU sequences from *Mallomonas caudata* and putative relatives. Numbers near each clade refer to maximum likelihood and parsimony bootstrap values. Bars represent nodes with support values < 50%.

and 304 parsimoniously informative sites (28.0%). Within *M. caudata*, samples from Korea and USA differed by up to 5 bp (0.45% pairwise divergence). *M. caudata* and its close relative, *M. asumundiae*, differed by at least 149 bp (15% pairwise divergence). In the phylogenetic tree of the *rbc*L data, all six samples of *M. caudata* produced a strongly supported clade. However, the genus was not monophyletic (Fig. 2).

Ultrastructure

Mallomonas caudata is an ovoid to spindle shaped, unicellalur alga, which remains covered with distinctive body scales and bristles (Fig. 3A). Under scanning electron microscope, body scales have a large elongated or circular pore in the center of the posterior end of the scale. Bristles are serrated on one side with minute teeth (Fig.

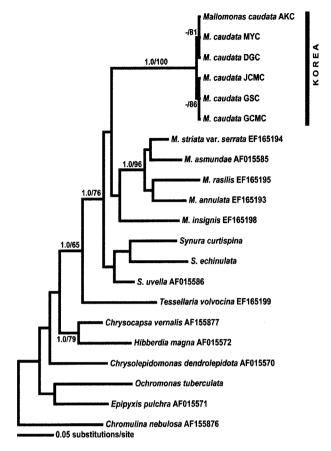


Fig. 2. ML tree of plastid rbcL sequences from *Mallomonas caudata* and putative relatives. Numbers near each clade refer to maximum likelihood and parsimony bootstrap values. Bars represent nodes with support values < 50%.

3B).

Cells are surrounded by body scales under TEM (Fig. 4A). The nucleus is placed in the center of the cell, but anteriorly at the longitudinal section (Fig. 4B). The nucleus is connected to the anteriorly inserted basal bodies by a rhizoplast (Fig. 4C-D). The connecting structures are fibrous roots that are distinct with extension from the basal body to the anterior part of the nucleus. These roots are composed of striated rootlets with covered part of the anterior surface of the nucleus (Fig. 4C-D). The microfibrillar and periodic structures of the rootlets of the rhizoplast are lined with nucleus and attached to a plate on the proximal section of the basal body at the top of the cell (Fig. 4E). There is a conspicuous incomplete collar of granular material around the fibres of the basal body-nucleus connector (Fig. 4D).

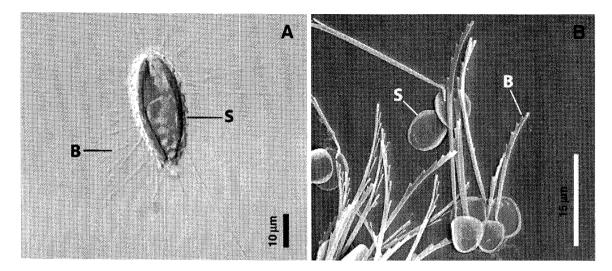


Fig. 3. *Mallomonas caudata*. A. Morphology of cell showing bristles (B) and scales (S) under light microscope. B. Detailed morphology of bristles (B) and scales (S) under scanning electron microscope.

DISCUSSION

Nuclear SSU and plastid *rbc*L data of *Mallomonas caudata* strains from Korea clearly show that this cosmopolitan planktonic species is genetically homogeneous. However, pairwise divergence of SSU sequences of samples between Korea and USA is higher than those of samples collected in Korea. Cosmopolitan species are often assemblages of diverge genetic lineages, as in *Synura petersenii* (Wee *et al.*, 2001). Additional studies using samples from Europe and USA will show the genetic variations among the allopatric populations of *Mallomonas*.

Protein-coding *rbc*L region is usually more variable than ribosomal SSU region in stramenopiles such as brown algae reported by us earlier (Boo *et al.*, 1999). Pairwise divergence of SSU sequences between *M. caudata* and *M. matvienkoae* ranged up to 1.2%. The sister relationship between these two species was also strongly supported in the phylogenetic tree. Lack of dome scales in both species is proposed as a plesiomorphic character of *Mallomonas* (Asmund and Kristiansen, 1986; Lavau *et al.*, 1997).

Morphology of *Mallomonas caudata* isolated from Korea is very similar to that of the species present in freshwater bodies of USA and Europe (Asmund and Kristiansen, 1986; Siver, 1991). Ultrastructure of the scales and bristles of the strains isolated from different reservoirs is very

similar and recognizable difference lacked between specimens from Korea and Europe. The large pore in the center of the posterior end of the scale is mostly elongated shape and rarely observed as circular.

TEM studies of Mallomonas caudata have shown the existence of striated roots, named rhizoplast, attached to the basal bodies. These structures are present in the Synurophyceae (Andersen, 1991) but are more prominent in the Mallomonas species (Brugerolle and Mignot, 2003). The rhizoplast is composed of microfibrils organized in striated rootlets attached to the multilayered plate of basal bodies and arranged on the surface of the nucleus at their distal ends. According to the ultrastructural studies, the rhizoplast of Synurophyceae constitutes a basal body-nucleus connector, typical to Synura (Andersen, 1985). The semicircular collar of granular material surrounding the rhizoplast is found in M. caudata, as reported in M. fastigiata (Brugerolle and Mignot, 2003). In this structure, *Mallomonas* is different from Synura uvella, which has naked rhizoplasts (Andersen, 1985). However, overall ultrastructure of the specimens of M. caudata from Korea is very similar to that of the cells from Texas, USA (Wujek, 1978).

Although cladistic analysis of scale morphology supported the monophyly of the genus, *Mallomanas* was divided into different groups in previous SSU data (Lavau *et al.*, 1997). In our study of SSU data, the genus was polyphyletic, dividing into

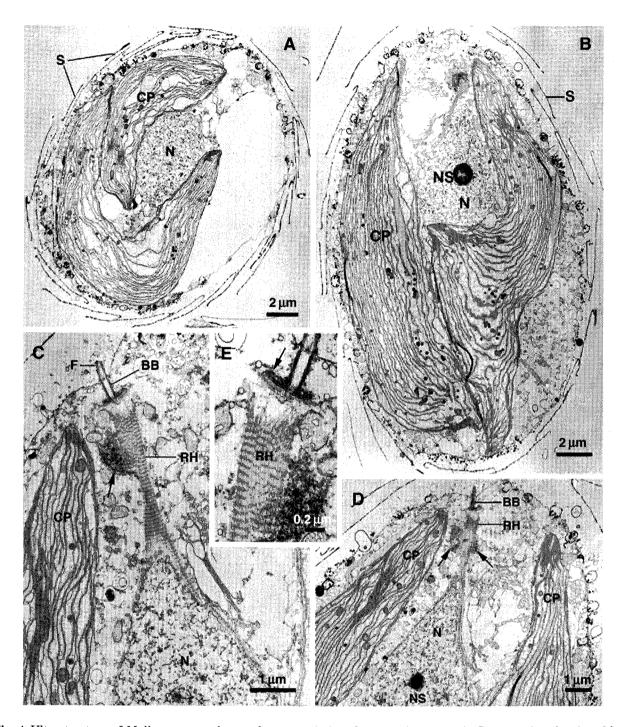


Fig. 4. Ultrastructure of *Mallomonas caudata* under transmission electron microscope. A. Cross section showing chloroplast (CP), nucleus (N), and scale (S) covering the cell. B. Longitudinal section showing nucleolus (NS), nucleus (N), chloroplast (CP), and scale. C-D. Serial sections showing basal body (BB), semicircular collar (arrows), and rhizoplast (RH) connecting between the basal body (BB) and nucleus (N). E. High magnification of the basal body region showing the microfibrillar and periodic structure of the rhizoplast (RH) attached to a plate (arrow).

several groups. In rbcL data, the strong clade existed among M. annulata, M. asmundiae, M. rasilis and M. striata excluded M. caudata and

M. insignis. The results imply that the current concept regarding *Mallomonas*, based on the nature of flagella and the colonial vs unicellular

nature (see review of Wee, 1997), should be reconsidered. The additional samplings of the genus from allover the world's aquatic bodies would give a better resolution on the phylogeny of *Mallomonas* with highlights on the classification of the genus.

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<국문적요>

한국산 *Mallomonas caudata* (Synurophyceae)의 미세구조, 핵 SSU 그리고 색소체 rbcL 유전자

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해양 같은 지리적 장벽에도 불구하고, 많은 담수조류는 세계의 다른 대륙에 서식하고 있다. 단세포 담수조류, Mallomonas caudata는 북반구의 미국, 유럽, 및 아시아에서 흔하며, 기후변화 감지나 수화현상 감시 같은 인간생활에 밀접하게 관련되어 있다. 본 종의 계통과 국내출현을 설명하기 위해여섯 군데의 저수지에서 채집된 균주로부터 엽록체 rbcL과 핵 SSU 유전자를 염기서열 분석하였다. 또한, 한국산 균주의 전자현미경적 구조를 조사하였다. 한국과 미국산 종의 SSU 염기서열은 0.06%가, rbcL은 0.45%의 차이로 거의 동일하였다. 두 유전자를 이용한 계통수에서 본 종은 속의다른 종들과 분명히 분리되지만, 단계통군은 아니었다. 근형질은 기저체의 다층판에 부착된 가로무 의의 microfibril들로 구성되어 있었으며, microfibril들의 끝은 핵의 표면 위에 배열되어 있었다. 이근형질은 Synurophyceae에서 전형적으로 보이는 기저체-핵 연결자이다. Mallomonas가 SSU와 rbcL자료에 의해 지지되지 않는 결과는 분류군 추가와 함께 좀더 연구되어야 할 것으로 사료된다.