

MORPHOLOGY AND MOLECULAR PHYLOGENY OF *AUREOPHYCUS ALEUTICUS* GEN. ET SP. NOV. (LAMINARIALES, PHAEOPHYCEAE) FROM THE ALEUTIAN ISLANDS¹

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A previously unknown species of kelp was collected on Kagamil Island, Aleutian Islands. The species can be easily distinguished from any known laminarialean alga: the erect sporophytic thallus is composed of a thin lanceolate blade attaining ~2 m in height and ~0.50 m in width, without midrib, and the edge of the blade at the transition zone is thickened to form a V-shape; the stipe is solid and flattened, slightly translucent, attaining ~1 m in length; the holdfast is semidiscoidal and up to 0.15 m in diameter. Anatomically, the blade has the typical trumpet-shaped hyphae characteristic of the Chordaceae and derived foliose laminarialean species (i.e., Alariaceae/Laminariaceae/Lessoniaceae). No hair pits or mucilaginous structures were observed on the blade or stipe. No fertile sporophytes were collected, but abundant juvenile sporophytes were observed in the field. In the molecular phylogenetic analyses using chloroplast *rbcL* gene, nuclear ITS1-5.8S-ITS2 rDNA, and mitochondria *nad6* DNA sequences, the new species (*Aureophycus aleuticus* gen. et sp. nov.) showed a closer relationship with Alariaceae of conventional taxonomy, or the “Group 1” clade of Lane et al. (2006) including *Alaria* and related taxa than with other groups, although the species was not clearly included in the group. *Aureophycus* may be a key species in elucidating the evolution of the Alariaceae within the Laminariales. Because of the lack of information on reproductive organs and insufficient resolution of the molecular analyses, we refrain from assigning the new species to a family, but we place the new species in a new genus in the Laminariales.

Key index words: Aleutian Islands; *Aureophycus aleuticus* gen. et sp. nov.; ITS1-5.8S-ITS2 rDNA;

Laminariales; molecular phylogeny; *nad6*; Phaeophyceae; *rbcL*

Abbreviations: EMAP, Environmental Monitoring and Assessment Program; ITS, internal transcribed spacer; ML, maximum likelihood; MP, maximum parsimony

The Aleutian Islands consist of a chain of volcanic oceanic islands separating the North Pacific Ocean from the Bering Sea and stretching from the North American continent nearly to Asia. Because of their geographic extent, the various islands experience somewhat different environmental conditions, including temperatures, precipitation, and ocean currents (Hultén 1937, Hunt and Stabeno 2005, Rodionov et al. 2005). Their shorelines are exposed to cold temperatures, high-energy wave surges, strong currents, ocean upwelling, and volcanic activity. Moreover, due to their remoteness and their harsh environments, these islands, especially the central and western Aleutian Islands (west of Samalga Pass) and including nearshore marine habitats, have been studied only sporadically.

The Aleutian Islands were first visited by Steller during the Bering expedition that discovered Alaska in 1741, but Steller’s collections did not survive the trip from Kamchatka to St. Petersburg (Shetler 1967). Later, scientists affiliated with various Russian expeditions visited the islands, especially the area around Unalaska Bay on Unalaska Island in the eastern Aleutians; records from these collections were published primarily by Postels and Ruprecht (1840) and Ruprecht (1850). A recent paper by Wynne (2006) describes one of the earliest known collections from Unalaska by Merck in 1790–1791. Unalaska was also visited by Setchell and colleagues during the University of California Botanical Expedition to Alaska in 1899 (Setchell and Gardner 1903). Kobayashi collected seaweeds in the Aleutian

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Islands in 1931 (Okamura 1933). R. F. Scagel, at the University of British Columbia, sponsored several expeditions to the islands in the 1960s, and collections from those trips provided records for the studies of kelps by Druehl (1968, 1970), Markham (1972), and Widdowson (1971). Intensive studies of the biota and ecology in relation to the atomic tests at Amchitka Island in the 1960s and 1970s resulted in the description of new and interesting marine algae occurring there (Wynne 1970a,b, 1980a,b, 1981, 1985a,b, 1987, 1990, Lebednik 1976, Athanasiadis et al. 2004). More recent visits and collections were made by N. Masuda (Lee 1977, Lee and Kurogi 1978, Masuda 1978) and Miller (Miller and Estes 1989, Masuda and Miller 1999).

The Alaska Department of Environmental Conservation in collaboration with the U.S. Environmental Protection Agency (U.S. EPA) has implemented the Environmental Monitoring and Assessment Program (EMAP) throughout the coastal waters of Alaska to assess the status and trends of significant ecological systems in the United States (U.S. EPA 1997). During the summers of 2006 and 2007, ~50 random EMAP sites were surveyed across the Aleutian Islands using scientific divers to photograph and collect marine life, including undescribed taxa, in the shallow nearshore (<20 m depth). In this article, we describe a new genus and species of kelp from a unique habitat in the central Aleutian Islands.

MATERIALS AND METHODS

Sporophytes of the new species were collected at Kagamil Island in the Islands of Four Mountains, Aleutian Islands, Alaska, by SCUBA (Fig. 1). Specimens were pressed on herbarium sheets on site. A part of the sporophytes was quickly dried in silica gel, and this was used for molecular analyses. For anatomical studies, fragments from the holotype specimen and from a silica-gel-dried specimen were hand-sectioned and examined using MVX10 dissecting microscope (Olympus, Tokyo, Japan) and BX50 compound microscope (Olympus) with Nomarski optics, and photographed using VB-7,000 digital camera (Keyence, Tokyo, Japan).

For molecular phylogenetic study, genomic DNA was extracted from the silica-gel-dried algal tissue using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany), following the manufacturer's instructions. PCR amplifications of the chloroplast RUBISCO LSU (*rbL*), the nuclear internal transcribed spacer region and 5.8S rRNA gene (ITS + 5.8S rDNA), and the mitochondria NADH dehydrogenase subunit 6 gene (*nad6*) were carried out with the GeneAmp PCR Cyclor 9700 (Applied Biosystems, Foster City, CA, USA) and the TaKaRa PCR Thermal Cyclor Dice (Takara Shuzo, Shiga, Japan) using a TaKaRa ExTaq (Takara Shuzo) reaction kit. Primers used for PCR and sequencing are listed in Table 1. The profiles of PCR reactions were identical to those described previously (Kawai et al. 2007). After polyethylene glycol (PEG) purification (Lis 1980), PCR products were sequenced using the CE DTCS Quick Start Kit (Beckman Coulter, Fullerton, CA, USA) and the CEQ8000 DNA analysis system (Beckman Coulter) according to the manufacturer's instructions. For the molecular phylogenetic analyses, published and newly determined sequence data of the Laminariales were used (Table S1 in the supplementary material). *Chorda filum* was chosen as the outgroup following Lane et al. (2006). Alignments were

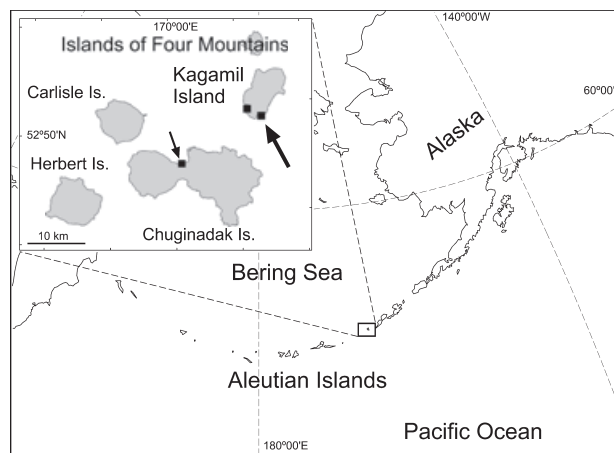


FIG. 1. Map showing the collection sites of *Aureophycus aleuticus* gen. et sp. nov. Large arrow shows the locality where attached plants were found, and small arrow shows the locality where the drift plant was found.

prepared using the CLUSTAL X computer program (Thompson et al. 1997) and then manually adjusted prior to phylogenetic analyses. To be comparable to the phylogenetic analyses of Lane et al. (2006), three different alignments were constructed for analyses here: (i) chloroplast *rbL* (1,392 bp); (ii) nuclear ITS1, 5.8S rDNA, and ITS2 (506 bp) excluding the ambiguous alignment regions; (iii) combined sequences of (i) and (ii) and mitochondrial *nad6* (total 2,834 bp). For the last data set, analyses using all three codons, as well as only the first and second codons, were carried out considering the saturation of the third codon as noted in Lane et al. (2006).

The aligned sequences were subjected to maximum parsimony (MP) analyses in a general heuristic search using PAUP* v. 4.0b10 (Swofford 2002). Ten thousand random additions of taxa were performed in each heuristic search, using the tree-bisection-reconnection (TBR) branch-swapping option. Gaps were not taken into account in analyses. The program Modeltest v. 3.06 (Posada and Crandall 1998) was used to find the model of sequence evolution that best fit the data set by the hierarchical likelihood ratio tests (hLRTs). When the best sequence evolution model had been determined for each data set, maximum-likelihood (ML) analyses were performed with PAUP* using the estimated parameters (substitution model, gamma distribution, proportion of invariable sites), with 100 random additions in a heuristic search. The robustness of the resulting phylogenies was tested by bootstrap analyses with 1,000 (MP) and 100 (ML) resamplings (Felsenstein 1985). Bayesian analyses were performed using MrBayes v3.0b4 (Huelsenbeck and Ronquist 2001). For the data sets 1 and 2, a substitution model was deduced with hLRT using MrModeltest 2.1 (Nylander 2004). The Bayesian analyses were initiated with a random starting tree and ran four chains of Markov chain Monte Carlo iterations simultaneously for 1,000,000 generations (data set 1) and 1,500,000 generations (data set 2), keeping one tree every 100 generations. The first 1,000 trees (data set 1) and 1,500 trees (data set 2) were discarded as burn-in, and the remaining trees were used to calculate a 50% majority rule tree and to determine the posterior probabilities. For data set 3, alignment was partitioned by region (*rbL*, ITS and 5.8S rDNA, and *nad6*), and substitution models with parameters were deduced for each region using Kakusan 2.0 (Tanabe 2007). The Bayesian analyses were performed as above, but the generations were 2,000,000. The first 2,000 trees were discarded, and the

TABLE 1. List of primers used for PCR and sequencing.

Code	F/R	Sequence (5'-3')	Annealing position
18F ^a	F	AAGGTGAAGTCGTAACAAGG	18S (1,768–1,787)
5.8F-1 ^a	F	ACGCAGCGAAATGCGATACG	5.8S (47–66)
ITS2-m	R	CGCTTTGCTGCGTCTTCAT	5.8S (59–39)
26R-1 ^a	R	GTTAGTTTCTTTCTCCGCG	26S (70–51)
nad5-P1	F	GGYCTTATHGARAGTTTAGG	<i>nad5</i> (1,774–1,793)
nad6-P2	R	AGTCACATAAATGATKCCAC	<i>nad6</i> (598–579)
nad11-P1	R	GCYTGRCAAGCYTGWATAAC	<i>nad11</i> (74–55)
rbcL-P2 ^b	F	GAWCGRACTCGAWTWAAAAGTG	<i>rbcL</i> (19–40)
U-rbc-R2.5	R	CCTTCATAAACAACACG	<i>rbcL</i> (587–571)
rbcL-Rh3 ^c	F	TTAAYTCTCARCCDITYATGCG	<i>rbcL</i> (629–650)
Ral-R952 ^b	R	CATACGCATCCATTTACA	<i>rbcL</i> (969–952)
rbcL-P1 ^b	F	GKGTWATTTGTAARTGGATGCG	<i>rbcL</i> (944–965)
rbcL-P3	F	CARTTYGGWGGWGGTACDATTGG	<i>rbcL</i> (1,210–1,232)
rbcS-P1 ^b	R	GGATCATCTGYCCATTCTACAC	<i>rbcS</i> (122–101)

Annealing positions correspond to the sequences of *Scytosiphon lomentaria* (Lyngbye) Link (18S rDNA, 5.8S rDNA and 26S rDNA, D16558: Kawai et al. 1995), *Laminaria digitata* (*nad5*, *nad6* and *nad11*, AJ344328: Oudot-Le Secq et al. 2002), and *Ectocarpus siliculosus* (Dillwyn) Lyngbye (*rbcL* and *rbcS*, X52503: Valentin and Zetsche 1990).

^aKawai et al. (2001).

^bKawai et al. (2007).

^cHanyuda et al. (2004).

remaining trees were used to calculate a 50% majority rule tree and to determine the posterior probabilities.

RESULTS

Habitat. To date, *A. aleuticus* gen. et sp. nov. has been found only in the central Aleutian Islands. Attached plants were observed only on Kagamil Island; a single drift specimen was found on Chuginadak Island (Fig. 1). Kagamil and Chuginadak islands are part of a volcanic island group known as the Islands of Four Mountains. The plants were observed at only two sites on Kagamil Island despite an extensive search around the island. Except for the single drift specimen on Chuginadak Island, the species was not observed elsewhere, including nearby Carlisle Island, or at any of the approximately four dozen other sites that were sampled across the Aleutian chain.

Due to the remarkably clear waters at Kagamil Island (up to 40 m visibility), this new kelp (Fig. 2a) was discovered by simply peering into the water from a small skiff cruising the shoreline. The brilliant sulfur-yellow edges of the kelp (Fig. 2b) were easily observed from the surface. *A. aleuticus* occurred only in the shallow subtidal (5 m depth) attached to large boulders that were scattered throughout a sandy area (Fig. 2, b and c). Algal species observed among *A. aleuticus* were *Cymatohaere triplicata*, *Saccharina subsimplex*, and *Porphyra variegata*. This site would be classified as a semiexposed habitat due to its significant fetch and the observed ground swell beating the shore.

Kagamil Island is unique among the Islands of Four Mountains because thermal activity is visible along the shoreline in the form of smoke stacks, steam, and gases issuing from the ground, and the

strong smell of sulfur in the air. Gaseous bubbles were observed percolating up through nearby *Druethlia fistulosa* beds, and divers reported warm sand as they surveyed the bottom. The warm sand was in strong contrast to very cold water temperatures commonly occurring in the central Aleutians even in summer. We collected hydrographic data at four stations in the Islands of Four Mountains, and Kagamil Island had the lowest near-surface temperature (4.9°C), pH (7.85), and dissolved oxygen (60% DO), and the highest salinity (33.2 ppt) among those stations. These values indicate an intense upwelling signal, consistent with oceanographic surveys conducted in the area in 2001 and 2002 (Ladd et al. 2005).

Habit and gross morphology. The sporophyte is composed of a discoidal, semi-cushion-shaped holdfast, flattened stipe, and simple blade (Fig. 2, a–d). The golden yellow holdfast can reach 15 cm in diameter and, although tightly attached to the substrate, is free from the substrate at its margin (Fig. 2, c and d). The golden yellow stipe is 0.5–1.0 m in length, rectangular and solid in cross-section, very strong, and slightly translucent. The blade is lanceolate, smooth and flat, up to ~2 m in length, 0.15–0.50 m in width in the broadest part, medium (“*Alaria*”) brown, and relatively thin. It lacks a midrib, but toward the base of the blade, the edges are reinforced or raised in a V-shape, which appears golden yellow in the water. There are subtle striations in the blade, very strong and stretchy monofilaments running lengthwise within the blade. Juvenile thalli to 5 cm in length were observed around the holdfasts of some adult thalli; the juveniles had the distinctive V-shape of the adults and were iridescent. Larger thalli were occasionally observed as epiphytes on the blades and stipes of other kelps.

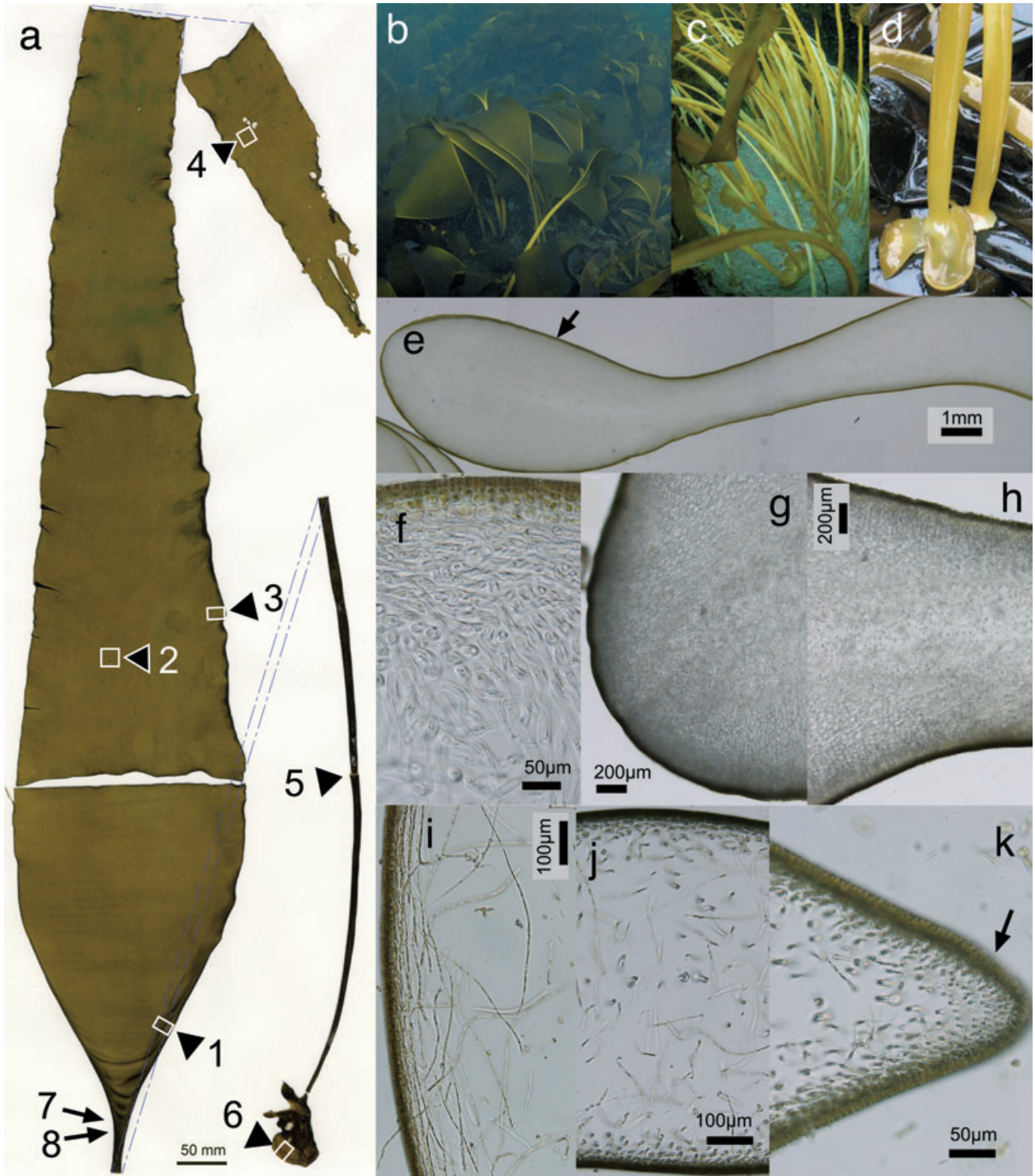


FIG. 2. Habit and morphology of *Aureophycus aleuticus* gen. et sp. nov. (a) Gross morphology of sporophyte (image reorganized from the scanned images of the holotype specimen cut and mounted on three herbarium sheets: UBC A85831 collected on July 15, 2006; anatomy based on the holotype specimen). The numbers show the positions of the sections for the anatomical observations (see below). (b) Population of sporophytes. (c) Stipes and holdfasts attached to boulders in sand. (d) Detached discoidal holdfasts. (e–h) Cross-section of the blade at position 1 in (a), showing the thickened margin (arrow). (f) In higher magnification showing the epidermal layer and cortical layer. (g) Marginal part and (h) transitional part from the thickened margin to the inner, thinner part of the blade. (i, j) Longitudinal section (i) and cross-section (j) of middle part of the blade at position 2 in (a). (k) Cross-section of the margin (arrow) of the blade at position 3 in (a).

Anatomy. The blade is composed of small, densely pigmented peripheral (epidermal) cells; less pigmented cortical cells; and loose medullary filaments, including the trumpet-shaped hyphae characteristic of the Chordaceae and the derived foliose laminarialean species (Figs. 2, e–k; 3, b and c). No hairs or mucilaginous structures (ducts or gland cells) were observed on the blade (Figs. 2, e–k; 3, a–c) or stipe (Fig. 3d). The margin of the lower part of the blade (Fig. 2, e–h) is remarkably thicker than the middle part and composed of densely

packed inner filaments (Fig. 2g). The lower part of the transitional zone (lower part of V-shape) is composed of densely packed cortical filaments and densely packed medullary filaments (Fig. 3f). The medullary layer is somewhat wider (and thereafter the cortex layer is thinner) at the margins in the upper part of the stipe underneath the V-shape. The middle part of the blade is ~1 mm thick and filled with loose, fine filaments, including trumpet-shaped hyphae, and its margin is wedge-shaped in cross-section (Fig. 2, i–k). The upper part of the

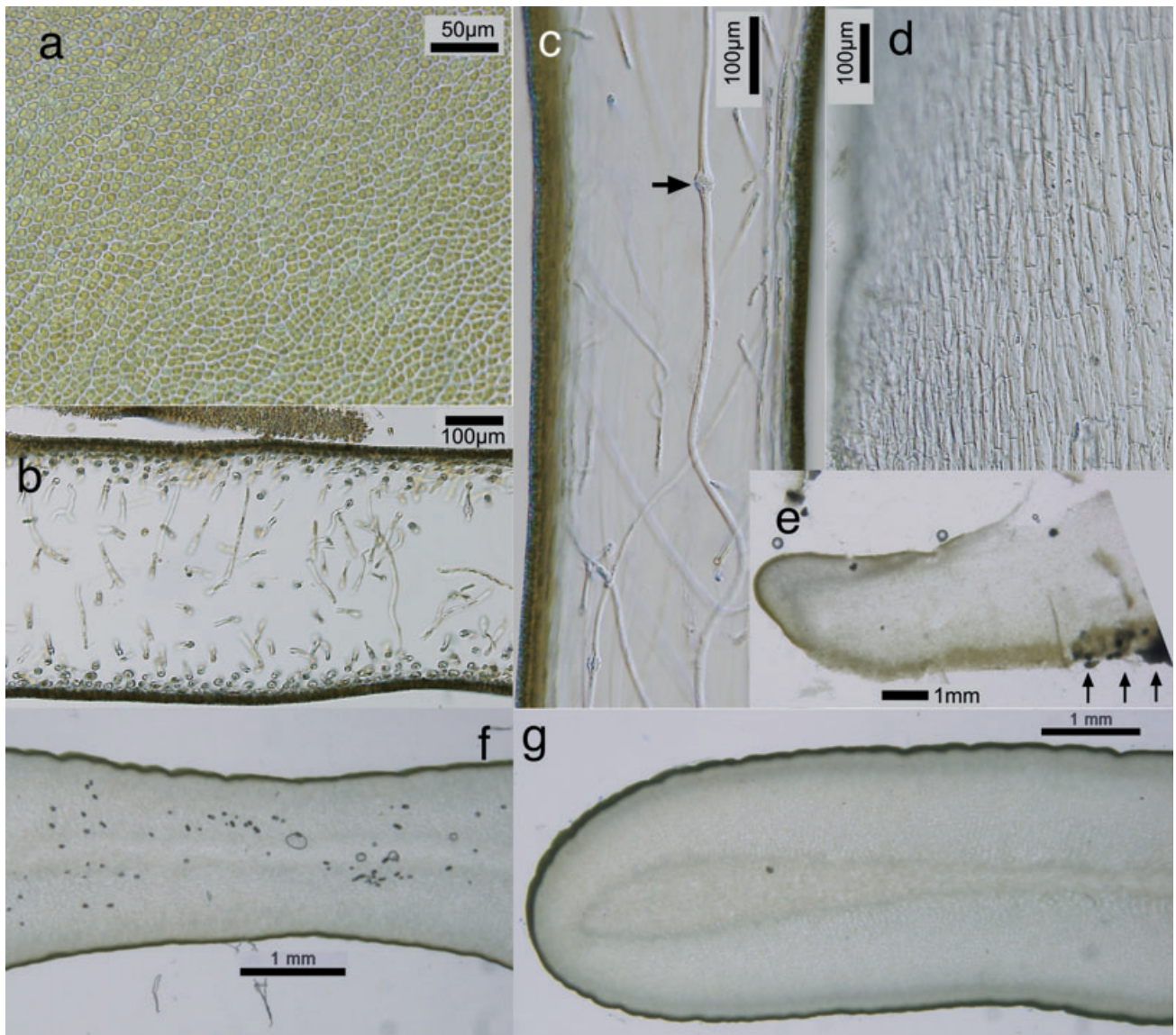


FIG. 3. Anatomy of *Aureophycus aleuticus* gen. et sp. nov. (a–e) Holotype specimen UBC A85831; (f and g) silica-gel-dried specimen ALEUT07-421 collected on 19 July 2007. (a) Surface view near the middle part of the blade. (b and c) Cross-section (b) and longitudinal section (c) of the distal part of the blade at position 4 in (a). Arrow shows the trumpet-shaped hyphae characteristic of derived Laminariales. (d) Longitudinal section of the stipe at position 5 in (a). (e) Longitudinal section of the holdfast (position 6 in a). Arrows show where the holdfast attaches to the substrate. (f) Cross-section of the lowermost part of the blade (lower part of the V-shape; corresponding to position 7 in [a] but of the specimen ALEUT07-421). (g) Cross-section of the uppermost part of the stipe just under the V-shape; corresponding to position 8 in (a).

blade is rather thin (<0.5 mm) and filled with fine, loose filaments, including trumpet-shaped hyphae (Fig. 3, b and c). The stipe is composed of densely packed filaments of long cylindrical cells (Fig. 3d). No fertile sporophytes have been collected thus far, and sporophylls, including primordial, have not been observed. The cushion-shaped holdfast is composed of densely packed short colorless cells and tightly adheres to the substrate (boulders) at its lower surface (Fig. 3e).

Molecular phylogeny. In the ML molecular phylogenetic analyses using *rbcL*, nuclear ITS1-5.8S-ITS2 ribosomal, and the combined dataset including *nad6* DNA sequences (Figs. 4–6, respectively), the new species showed a closer relationship with the Alariaceae clade of conventional taxonomy (i.e., *Alaria marginata*, *D. fistulosa*, *Undaria pinnatifida*, *Pleurophycus gardneri*, and *Pterygophora californica*) plus *Lessoniopsis littoralis*, or the “Group 1” clade (=Alariaceae) in Lane et al. (2006) including all these taxa than with any other group. The bootstrap supports were generally similar in ML, MP, and Bayesian analyses for all of the data sets (Figs. 4–6). In the combined sequence data set (*rbcL*, ITS1-5.8S-ITS2, and *nad6*), the analysis using only the first and second codons of the *nad6* gene as in Lane et al. (2006) gave the same tree topology as the analysis using the all tree codons for the clade including the “Group 1” and *Aureophycus*; however, the bootstrap values supporting the branches were lower in the former data set (data not shown). *A. aleuticus* was basal to the “Group 1” clade in all of the data sets, but the relationships between the

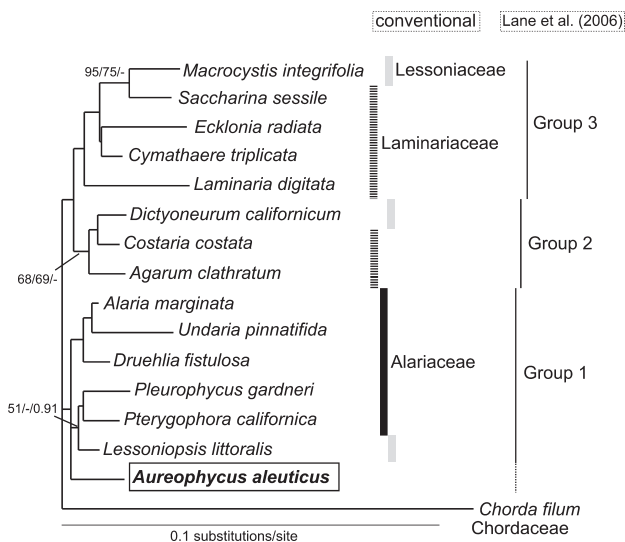


FIG. 4. Maximum-likelihood (ML) tree based on the chloroplast *rbcL* gene. Numbers on the branches indicate bootstrap values from ML analysis (left) and maximum-parsimony (MP) analysis (center), and posterior probabilities from Bayesian analysis (right). Only bootstrap values >50% and posterior probabilities >0.90 are shown.

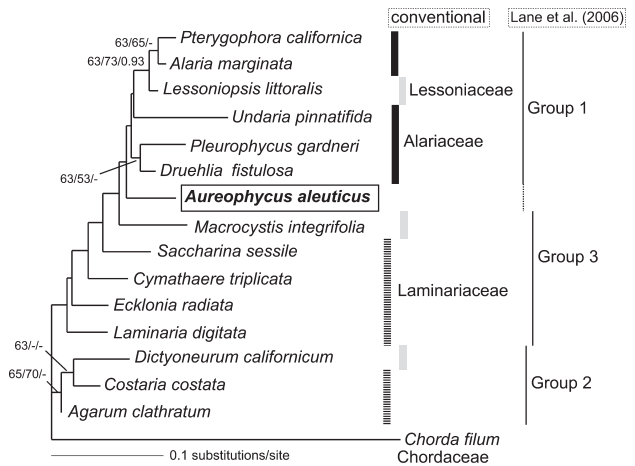


FIG. 5. Maximum-likelihood (ML) tree based on the sequences of nuclear 5.8S rRNA gene and ITS regions. Numbers on the branches indicate bootstrap values from ML analysis (left) and maximum-parsimony (MP) analysis (center), and posterior probabilities from Bayesian analysis (right). Only bootstrap values >50% and posterior probabilities >0.90 are shown.

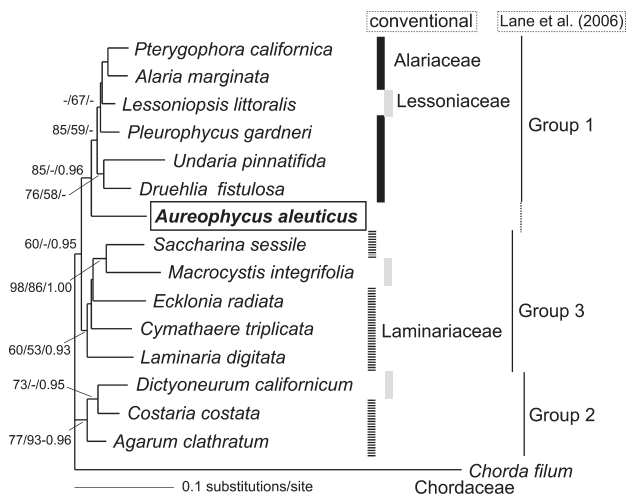


FIG. 6. Maximum-likelihood (ML) tree from the combined total alignment (nuclear 5.8S rRNA gene and ITS region, chloroplast *rbcL* gene, and mitochondria *nad6* gene). Numbers on the branches indicate bootstrap values from ML analysis (left) and maximum-parsimony (MP) analysis (center), and posterior probabilities from Bayesian analysis (right). Only bootstrap values >50% and posterior probabilities >0.90 are shown.

Alariaceae, Lessoniaceae, and Laminariaceae of conventional taxonomy or the three groups of Lane et al. (2006) were not clearly resolved: the closer phylogenetic relationship of “Group 2” (=Costariaceae) and “Group 3” (=Laminariaceae) than either with “Group 1” was suggested in the *rbcL* tree (Fig. 4), but “Group 1” appeared closer to “Group 3” in the nuclear ITS5.8S rDNA tree (Fig. 5) and in the combined sequence data set including mitochondrial *nad6* (Fig. 6). In the Bayesian analyses,

the phylogenetic position of *Aureophycus* was identical to that of ML analyses, except for *rbcL* tree. In contrast, in the MP analyses, the phylogenetic position of *Aureophycus* was not clearly resolved: the bootstrap values supporting most of the branches connecting *Aureophycus* with other taxa were <50%, and the tree topologies were different depending on the gene markers.

Aureophycus aleuticus H. Kawai, T. Hanyuda, Lindeberg et S. C. Lindstr., sp. et gen. nov. (Figs. 2 and 3).

Description and diagnosis. Sporophytum e lamina lanceolata, stipite complanato, et haptero discoideo constans; lamina tenuis membranacea usque ad 2 m longa, ad zonam transitionalem limbo incrassato litteram V elevatam formante instructa, sine undulationibus, filis tenuibus laxis necnon hyphis tubaeformibus impleta; stipes rectangularis solidus parum translucens, 1 m longitudine attingens; hapteron hemidiscoideum usque ad 0.15 m diametro. Nec organa mucosa nec pili praesentes. Sporophy- tum fertile ignotum.

Haec species a speciebus laminarilibus affinis forma characteristica sporophytorum, haptero discoideo et lamina tenui zona transitionali incrassata V-forma, et ordinibus peculiaribus nucleotidorum rADN *rbcL* et ITS (ordine rADN *rbcL* AB355025, rADN ITS AB355026) distinguenda.

Sporophyte composed of a lanceolate blade, flattened stipe and discoidal holdfast; the blade thin, membranous, up to 2 m in length, with obvious thickened rim at the transition zone forming a raised "V," without undulations, filled with fine, loose filaments including trumpet-shaped hyphae; the stipe rectangular, solid, slightly translucent, reaching 1 m in length; the holdfast semidiscoidal, up to 0.15 m in diameter. No mucilage organs or hairs present. Fertile sporophyte unknown.

The species is distinguished from related laminarialean species in having characteristic sporophyte morphology with discoid holdfast and thin blade with V-shaped thickened transition zone, and its distinctive nucleotide sequences of *rbcL* and ITS rDNA (*rbcL* rDNA sequence AB355025 and ITS rDNA AB355026).

Named after the prominent golden-yellow color of the V-shaped rim at the transition zone of the blade and stipe for the generic name, and the geographic distribution of the taxon for the species epithet. The species has been given the common name Golden V kelp by those who have seen it in the field.

Holotype: UBC A85831, Kagamil Island (52°57'07" N, 169°43'02" W), Island of Four Mountains, Aleutian Islands, Alaska (USA), 5 m below MLLW, July 15, 2006.

Isotype: A85832.

Known distribution: Kagamil Island, Aleutian Islands, Alaska, USA.

DISCUSSION

The order Laminariales is thought to have originated on the northwestern coast of the Pacific Ocean and then to have expanded and diverged eastward along the Bering Sea and Aleutian Islands to the northeast Pacific and northward through the Arctic Ocean to the Atlantic Ocean. This scenario is based on a number of lines of evidence: (i) the basal-most taxa of the order, namely, Akkesiphyceae and Pseudochordaceae, are distributed only in the northwest Pacific around the Okhotsk Sea (Kawai and Kurogi 1985, Kawai 1986, Kawai and Nabata 1990); and (ii) the Chordaceae, the sister group of the advanced (foliose) Laminariales (i.e., Alariaceae/Laminariaceae/Lessoniaceae), has higher species and genetic diversities in the northwest Pacific (Lüning and Tom Dieck 1990, Kawai et al. 2001, Sasaki and Kawai 2007). On the other hand, the nearly equal species and generic diversity of the advanced Laminariales on the two sides of the North Pacific (Lane et al. 2006) indicate that both regions have been involved in its diversification, as previously argued by Estes and Steinberg (1988) and Stam et al. (1988).

Samalga Pass, the area where *Aureophycus* was discovered, appears to represent a distinct boundary both physically and biologically (Heifetz et al. 2005, Ladd et al. 2005). Samalga Pass is the first deep channel as one moves westward along the Aleutian chain (Hunt and Stabeno 2005). Passes to the east are shallow, narrow channels that connect continental shelves 10–100 km wide to the north and south. At Samalga Pass and westward to Kiska Island, the islands of the chain are perched on narrow shelves separated by deep, wide channels. These islands of the central Aleutians have therefore been islands even during the lowered sea levels of Pleistocene glaciations and have thus been isolated for a significant period of time. Moreover, recent studies have revealed a clockwise circulation around some of the Islands of Four Mountains, suggesting a further isolating mechanism (Ladd et al. 2005). These observations suggest that *Aureophycus* may have been isolated in this part of the Aleutian chain for a significant amount of time and may in fact have a very limited distribution and population size. If true, this would help explain its divergent position in all the molecular phylogenies.

The occurrence of *A. aleuticus* in a volcanically active area is not unique. *Undariella kurilensis*, another relatively newly described genus and species of Alariaceae, was recorded from a similar habitat in the Kurile Islands by Petrov and Kussakin (1997). We did not examine whether the bright yellow stipe and margin of *Aureophycus* was related to elevated sulfur concentrations due to significant venting where it lives.

The construction of the thin, large (exceeding 2 m) blade supported by the thickened transition

zone as seen in *Aureophycus* is unique in Laminariales and interesting from a mechanical point of view. The anatomy of the thin blade filled with loose filaments and lacking tightly adhered, dense subcortical filaments resembles that of blades of *Alaria*, *Undaria*, and *Postelsia*, and so forth. However, the blades of *Alaria* and *Undaria* are physically reinforced by midribs, and those of *Postelsia* are relatively small. In contrast, species having large lanceolate blades (e.g., *Laminaria*, *Lessoniopsis*, etc.) have tightly adhered, dense subcortical filaments to maintain the strength of the blade.

Although reproductive sporophytes, which are likely to occur later in the season, as is common in kelps, have not been collected, and hence the reproductive structures are not yet known, the gross morphology of the erect thallus composed of a large blade and stipe and anatomical structures provided with trumpet-shaped hyphae clearly indicate that this species belongs to the order Laminariales and the so-called Alariaceae/Laminariaceae/Lessoniaceae group of families. Considering the distinctive morphology of the sporophyte with its relatively thin blade, the prominent, characteristic V-shaped margin at the transition zone, and the unique habitat in a volcanic area of the Aleutian Islands, it is also clear that this is an undescribed taxon. The molecular phylogenetic data using the chloroplast *rbcl*, nuclear ITS1-5.8S-ITS2 ribosomal sequence, and the mitochondrial *nad6* gene all indicate that the species has not been included in any of the known laminariales genera studied to date despite the comprehensive studies of Yoon et al. (2001) and Lane et al. (2006). The systematic position of the species deduced from the molecular analyses differs somewhat depending on the molecular marker, but all suggest a closer phylogenetic relationship with the "Group 1" clade (=Alariaceae) of Lane et al. (2006) than with other groups. Since most of the members of "Group 1" (which represents a revised Alariaceae) form sporophylls as reproductive structures, it is therefore possible that *A. aleuticus* also forms sporophylls when it becomes fertile, although a blade location (as occurs in *Pleurophycus gardneri*) is also possible. The insufficient resolution of the genetic markers in the molecular analyses for elucidating familial level phylogeny of laminariales species forces us to forego familial assignment of *A. aleuticus*, but we suggest placing it in its own new genus in the Laminariales closely related to the "Group 1" taxa of Lane et al. (2006), representing the Alariaceae.

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Supplementary Material

The following supplementary material is available for this article:

Table S1. Sources of sequence data used in the phylogenetic analyses.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1529-8817.2008.00548.x>.

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