

Molecular and morphological evidence for the taxonomic status of a newly reported species of *Albula* (Albuliformes: Albulidae) from Korea and Taiwan

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To clarify the taxonomic status of five specimens of *Albula* collected from Korea and Taiwan (*Albula* sp.), genetic differences among them and other congeneric species were investigated based on mitochondrial DNA cytochrome *b* sequences. All five specimens of *Albula* sp. showed identical haplotypes and strongly supported a monophyletic group on phylogenetic analysis. The genetic differences between *Albula* sp. and ten other species of *Albula* ranged from 0.100 to 0.164. These values were almost equal to or exceeded the interspecific differences among the latter ten species (0.038–0.206). Morphological comparisons of *Albula* sp. and another four Indo-Pacific species, *A. argentea*, *A. glossodonta*, *A. oligolepis* and *A. virgata*, are also presented. *Albula* sp. could be distinguished from the latter four species in their numbers of pored lateral-line scales, anal fin rays and vertebrae, as well as in several proportional measurements.

Keywords: *Albula* sp.; bonefish; morphology; mitochondrial DNA; cytochrome *b*

Introduction

Bonefishes genus *Albula* Scopoli 1777 (Albulidae: Albuliformes) are distributed globally in tropical and subtropical coastal areas (Hildebrand 1963; Pfeiler et al. 2006; Randall 2005; Nelson 2006). Although *Albula* had been considered to contain only two species, *A. vulpes* (Linnaeus, 1758) and *A. nemoptera* (Fowler, 1911), eight valid species are recognized worldwide. Among them, four species occur in the Indo-Pacific region, *A. argentea* (Forster in Bloch and Schneider 1801), *A. glossodonta* (Forsskål, 1775), *A. oligolepis* Hidaka, Iwatsuki and Randall 2008, and *A. virgata* (Jordan and Jordan, 1922) (Hidaka et al. 2004, 2008), whereas *A. esuncula* (Garman, 1899) and *A. pacifica* (Beebe, 1942) are known from the eastern Pacific, and *A. nemoptera* and *A. vulpes* from the western Atlantic (Smith 2002; Pfeiler 2008; Pfeiler et al. 2008). Two other species (*Albula* sp. A–B) have been proposed based on their genetic and distributional characteristics (Colborn et al. 2001; Bowen et al. 2008), their identities are, however, still alive.

In Korea, although Mori (1952) first recorded *A. vulpes* in a checklist of Korean fishes, Kim et al. (2005) regarded the species to be *A. neoguinaica* (Valenciennes in Cuvier and Valenciennes 1847). Kim et al. (2008) then documented the occurrence of a leptocephalus at Jeju Island and analysed its mitochondrial (mt) DNA cytochrome *b* gene (*cyt b*) sequence,

thus identifying the leptocephalus as *A. forsteri* (Valenciennes in Cuvier and Valenciennes 1847). In Japan, two bonefishes are known to date. A single species, given the scientific name *A. vulpes* by Matsubara (1955), has been recognized. Aizawa (2000) regarded the species as *A. neoguinaica*, whereas Hidaka et al. (2004) subsequently considered it to be *A. forsteri*. *A. glossodonta* has also been recorded for southern Japan by Hidaka et al. (2004). In China, Zhang (1984) reported a morphological description of *A. vulpes* from Fujian Province, but *A. vulpes* is currently known only from the western Atlantic, as noted above. In Taiwan, Shen et al. (1993) reported *A. glossodonta*, but no subsequent observations have been recorded. In recent years, Hidaka et al. (2008) confirmed *A. argentea* as valid, synonymizing both *A. neoguinaica* and *A. forsteri* with *A. argentea*, in their taxonomic review. However, Hidaka et al. (2008) did not recognize *A. argentea* in East Asia, regarding its distribution as restricted to the Philippines and southward. Therefore, the appropriate scientific identities of the species regarded as *A. vulpes*, *A. neoguinaica*, or *A. forsteri* in East Asia are currently unknown.

We collected five *Albula* specimens from the North-western Pacific (Korea and Taiwan). To clarify the taxonomic status of them, we investigated the genetic differences among them and with other species of *Albula* from throughout the world, on the basis of

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Table 1. List of nucleotide samples in the genus *Albula*.

Species	Locality	Accession number	Voucher number
<i>Albula</i> sp. ^a	Korea	HM119396	PKU 3394
<i>Albula</i> sp. ^a	Taiwan	HM119397-119400	ASIZP0067114, ASIZP0067133 ASIZP0067192, ASIZP0067194
<i>Albula esuncula</i> ^{c,e}	Panama	AF311760	ALB40
	Mexico	EF602158	A8
<i>Albula forsteri</i> ^b	Korea	EU555519	NIBR-P0000002382
<i>Albula glossodonta</i> ³	Hawaii	AF311768, AF311769	ALB61, ALB62
<i>Albula nemoptera</i> ^c	Brazil	AF311754, AF311755	ALB22, ALB23
<i>Albula oligolepis</i> ^c	Indo-Pacific	AF311770, AF311773	ALB77, ALB88
<i>Albula pacifica</i> ^d	Mexico	DQ272658, DQ272659	A15, A16
<i>Albula neoguinaica</i> ^c	Fiji	AF311765	ALB54
<i>Albula virgata</i> ^c	Hawaii	AF311764	ALB47
<i>Albula vulpes</i> ^c	Caribbean	AF311753, AF311771	ALB1, ALB7
<i>Albula</i> sp. A ^{c,e}	California	AF311758	ALB35
	Mexico	EF602156	AL05
<i>Albula</i> sp. B ^c	Atlantic	AF311751, AF311756	ALB10, ALB28

^a Present study; ^b Kim et al. (2008); ^c Colborn et al. (2001); ^d Pfeiler et al. (2006); ^e Pfeiler et al. (2008).

their mtDNA *cyt b* sequences. We also compared the morphological characters of *Albula* sp. with those of four congeneric species from the Indo-Pacific region reported by Hidaka et al. (2004, 2008).

Materials and methods

Genomic DNAs were extracted from the muscle tissues of the fish using 10% Chelex 100 Resin (Bio-Rad, Hercules, CA). The polymerase chain reaction (PCR) was used to amplify the mitochondrial DNA *cyt b* gene using primers H14803 (5'-TGCTAGGGTTGTGTT-TAATT-3') (Pfeiler et al. 2006) and albula-L (5'-GTCT CCAAGAAGGTTAGG-3'). PCR was conducted on a

thermal cycler (ABI 2720 Thermal Cycler, Foster City, CA), with PCR solutions containing 5–10 µl of genomic DNA, 2.5 µl of 10X PCR buffer, 2 µl of 2.5 mM dNTPs, 1 µl of each primer, 0.2 µl of FR *Taq* DNA polymerase (Biomedic, Korea) and 25 µl of distilled water. The PCR proceeded under the following conditions: initial denaturation at 94°C for 3 min, 30 cycles of denaturation at 94°C for 1 min, annealing at 50°C for 1 min, and extension at 72°C for 1 min, and a final extension at 72°C for 10 min. The amplification products of the target DNA were checked with agarose gel electrophoresis. The samples were purified using the Corebio™ Duo-PCR Purification Kit (Core Bio System Co. Ltd, Korea). DNA was sequenced on an ABI 3730XL Sequencer (Applied Biosystems Inc., Foster City, CA) using the ABI PRISM® BigDye™ Terminator v3.0 Ready Reaction Cycle Sequencing Kit (Applied Biosystems Inc., Foster City, CA). The nucleotide sequence data reported here have been submitted to the DDBJ/EMBL/GenBank nucleotide sequence databases (accession numbers HM119396–HM119400). For the molecular comparisons, we obtained the mtDNA *cyt b* sequences of other *Albula* species (Table 1) and two outgroups (*Elops saurus* and *Pterothrissus gissu*) from the NCBI (National Center for Biological Information) database.

Mitochondrial DNA *cyt b* sequences were checked and aligned using BioEdit ver. 7 (Hall 1999), and the genetic distances were calculated according to the Kimura two-parameter model (Kimura 1980) using MEGA4 (Tamura et al. 2007). Phylogenetic trees were inferred with the neighbour-joining (NJ) and maximum-likelihood (ML) methods. NJ analysis was conducted with the Kimura two-parameter model and

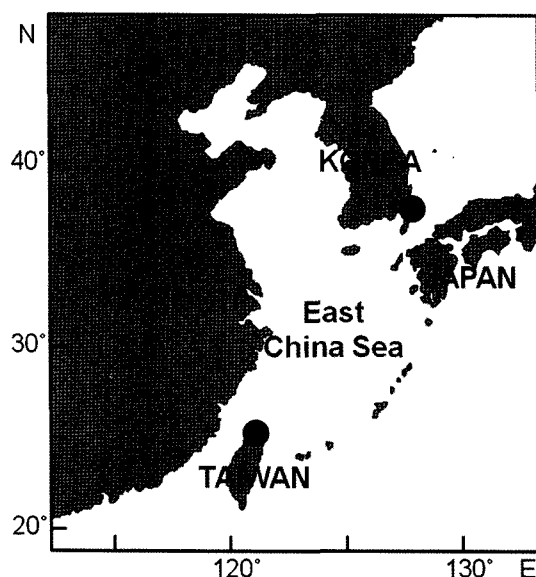


Figure 1. Sampling area (●) of *Albula* sp.

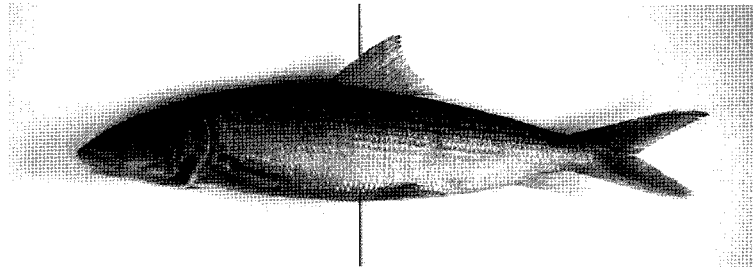


Figure 2. *Albula* sp., PKU3394, 350.1 mm SL, Gijang, Busan, Korea.

1000 bootstrap replications using MEGA4 (Tamura et al. 2007). ML analysis was conducted with the K81uf + I+G model, determined with Modeltest 3.7 (Posada and Crandall 1998; Posada and Buckley 2004),

with 100 bootstrap replications using PAUP 4.0b10 (Swofford 2002).

Counts were made according to Rivas and Warlen (1967) and measurements were made according to

Table 2. Meristic and morphometric characters of genus *Albula*.

	<i>Albula</i> sp. ^a	<i>Albula argentea</i> ^b	<i>Albula oligolepis</i> ^b	<i>Albula virgata</i> ^b	<i>Albula glossodonta</i> ^c
Number of specimens	5	30	36	39	28
Standard length (mm)	62.8–350.1	49–308	73–589	85–322	65–530
Counts					
Dorsal fin	18	17–18	17–19	17–18	17–18
Pectoral fin	16–18 (17.6)	16–18	17–19	17–18	17–19
Pelvic fin	10	10	10	10–11	9–10
Anal fin	9	8	7–9	8	7–8
Pored lateral line scales	77–80 (78.5, <i>n</i> = 2)	68–74	61–65	63–67	66–70
Scales above lateral line	9 (<i>n</i> = 4)	8–9	7.5–8	9–10	8–9
Scales below lateral line	6–7 (6.3, <i>n</i> = 4)	5–6	6	6–6.5	5–6
Predorsal scales	25 (<i>n</i> = 1)	17–24	18–25	22–26	21–23
Branchiostegal rays	13–15 (14.4)	12–15	12–15	13–14	12–14
Gill rakers	16 (<i>n</i> = 1)	17–25	16–22	18–21	18–23
Vertebrae	77–78 (77.4)	71–74	64–66	65–68	67–69
Measurements in% SL					
Body depth	16.6–22.0 (19.1)	16–25	18–23	18–22	16–31
Predorsal length	48.8–52.7 (50.7)	48–54	46–53	48–52	47–53
Prepectoral length	29.4–33.6 (31.4)	–	–	–	–
Prepelvic length	61.3–63.4 (62.4)	58–62	58–65	57–62	57–64
Preanus length	73.1–75.3 (74.3)	71–74	68–76	68–74	67–74
Depth of caudal peduncle	6.7–7.3 (6.9)	7–9	7–8	7–8	7–9
Length of caudal peduncle	11.8–13.4 (12.7)	9–13	9–12	11–12	9–13
Length of dorsal base	15.7–18.5 (16.8)	15–18	12–17	15–17	14–17
Length of anal base	5.5–7.4 (6.5)	5–8	5–6	5–6	5–6
Length of longest dorsal ray	16.9–18.9 (17.9)	17–19	14–19	17–20	17–22
Length of longest anal ray	6.5–10.3 (9.0)	8–10	7–14	9–10	8–10
Length of pectoral fin	16.4–17.2 (16.7)	15–18	14–17	16–18	15–19
Length of pelvic fin	12.7–13.8 (13.3)	13–15	12–14	13–16	12–15
Head length	28.8–35.8 (33.5)	28–32	28–32	26–31	28–30
Snout length	11.9–12.7 (12.3)	10–12	11–13	10–12	9–13
Postorbital length of the head	14.3–16.2 (15.1)	12–15	12–14	11–14	10–13
Suborbital width	2.5–4.4 (3.4)	2–4	3	2–3	2–4
Interorbital width	7.1–8.4 (7.7)	9–13	9–12	7–11	6–8
Length of eye	3.8–8.4 (6.9)	5–10	4–8	5–8	5–9
Length of upper jaw	11.6–14.6 (13.3)	10–12	10–13	9–12	8–11
Length of mandible	9.6–12.9 (11.5)	7–10	7–11	7–9	–

Table 2 (Continued)

	<i>Albula</i> sp. ^a	<i>Albula argentea</i> ^b	<i>Albula oligolepis</i> ^b	<i>Albula virgata</i> ^b	<i>Albula glossodonta</i> ^c
Preoral length	2.6–3.9 (3.4)	–	–	–	–
Length of last dorsal fin ray	6.3–7.8 (6.9)	6–8	5–8	6–8	6–8
Length of last anal fin ray	5.6–7.0 (6.2)	4–8	5–7	5–7	5–7
Body width	9.9–14.3 (11.7)	11–15	10–15	10–14	8–14
Preanal fin length	83.7–85.7 (84.4)	84–87	83–88	80–87	80–87
Upper caudal fin lobe length	23.9–26.6 (25.5)	27–31	23–30	26–31	27–35
Lower caudal fin lobe length	22.5–26.0 (24.5)	25–29	20–28	25–29	26–31
Width of mouth	7.2–8.2 (7.6)	7–11	7–10	8–10	–
Maxillary depth	2.0–3.2 (2.8)	2–4	2–5	2–4	–

^a Present study; ^b Hidaka et al. (2008); ^c Hidaka et al. (2004).

Rivas and Warlen (1967), Hubbs and Lagler (2004) and Hidaka et al. (2008). Measurements were made with a Vernier caliper to the nearest 0.1 mm, and all data were then converted to percentages of the standard length (SL). The number of dorsal fin rays, anal fin rays, vertebrae and teeth patch were taken from radiographs (X' Pert-MPD system, Netherlands; SOFTEX M60, Japan; SOFTEX HA-100, Japan). The last two dorsal and anal fin rays were counted separately and the hypural bone was included in the number of vertebrae, following Rivas and Warlen (1967).

Materials examined

PKU 3394, one specimen, 350.1 mm SL, 35°11'N 129°13'E, Sirang-ri, Gijang-gun, Busan, Korea, 31 October 2007, caught by J. K. Kim with a set net (Figures 1, 2). ASIZP 0067114, one specimen, 62.8 mm SL; ASIZP 0067133, one specimen, 69.1 mm SL; ASIZP 0067192, one specimen, 71.8 mm SL; ASIZP 0067194, one specimen, 96.2 mm SL, 25°2'N 121°65'E, Wanli, Taipei County, Taiwan, 15 June 2006, caught by D. F. Lee with a hook and line.

Results and discussion

A total of 524 base pairs (bp) of mtDNA *cyt b* sequences were obtained from the five specimens of *Albula* sp. and compared with those of other *Albula* species and two outgroups (*E. saurus* and *P. gissu*). All five specimens of *Albula* sp. had identical haplotypes. *Albula* sp. showed a biased nucleotide base composition, in that cytosine was least represented and thymine most represented (A = 19.5%, C = 19.3%, G = 22.5%, and T = 38.7%). Of the 524 bp sequences for eleven *Albula* species, 217 nucleotide sites were variable and 180 were parsimoniously informative. The Kimura two-parameter distances (*d*) ranged from 0.038 to 0.206 among the eleven *Albula* species. *Albula* sp. showed the lowest *d* value (0.100) with *Albula* sp. B and the highest *d* value (0.164) with *Albula oligolepis* (Table 3). The genetic distances (*d*) between *Albula* sp. and the other nine *Albula* species were 0.100–0.164, which are equal to or exceed the interspecific differences among the latter ten congeneric species (0.038–0.206) (Table 3). The NJ tree suggested eleven lineages, including the clade containing *Albula* sp., which was supported by a bootstrap value of 100% (Figure 4), and the ML tree also supported the monophyly of *Albula* sp. with a bootstrap value of 100% (Figure 5). These findings indicate that the *Albula* specimens represent a species distinct from the other congeneric species.

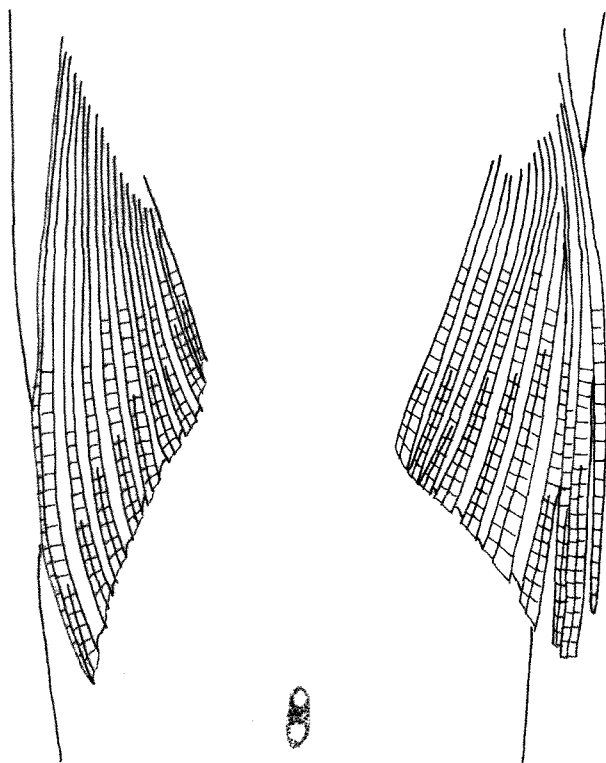


Figure 3. Magnification of abdominal area of *Albula* sp. Showing the pelvic fin that extends to the anterior margin of the anus.

Table 3. Interspecific genetic divergence among 11 *Albula* species with two outgroups based on mtDNA *cyt-b* sequences.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
1 <i>Albula</i> sp.													
2 <i>Albula argentea</i> *	0.162												
3 <i>Albula esuncula</i>	0.105	0.169											
4 <i>Albula glossodonta</i>	0.137	0.198	0.124										
5 <i>Albula nemoptera</i>	0.134	0.186	0.145	0.193									
6 <i>Albula oligolepis</i>	0.164	0.083	0.163	0.183	0.193								
7 <i>Albula pacifica</i>	0.135	0.168	0.147	0.189	0.041	0.167							
8 <i>Albula virgata</i>	0.154	0.038	0.168	0.206	0.183	0.080	0.166						
9 <i>Albula vulpes</i>	0.126	0.188	0.113	0.076	0.165	0.175	0.144	0.191					
10 <i>Albula</i> sp. A	0.125	0.175	0.057	0.147	0.175	0.169	0.154	0.185	0.131				
11 <i>Albula</i> sp. B	0.100	0.194	0.125	0.130	0.137	0.183	0.122	0.185	0.113	0.128			
12 <i>Elops saurus</i>	0.354	0.369	0.334	0.348	0.383	0.376	0.379	0.383	0.342	0.334	0.369		
13 <i>Pterothrissus gissu</i>	0.347	0.363	0.335	0.300	0.341	0.346	0.342	0.359	0.320	0.342	0.329	0.240	

*Including *Albula forsteri* and *Albula neoguinaica*.

Our molecular analysis revealed that *Albula* sp. does not correspond to the leptocephalus from Jeju Island, Korea, identified as *A. forsteri* by Kim et al. (2008). Instead, the mtDNA *cyt b* sequence of the leptocephalus from Jeju Island (GenBank accession number EU555519) corresponds to that of *A. neoguinaica* from Fiji (GenBank accession number

AF311765; Colborn et al. 2001, $d = 0.004$), indicating that the leptocephalus from Jeju Island may be *A. argentea*, a senior synonym for *A. neoguinaica*, as the northernmost record of the species. In the present study, we have confirmed that there are two species of *Albula* in Korea, *A. argentea* and *Albula* sp., apart from the species regarded as *A. neoguinaica* sensu Kim

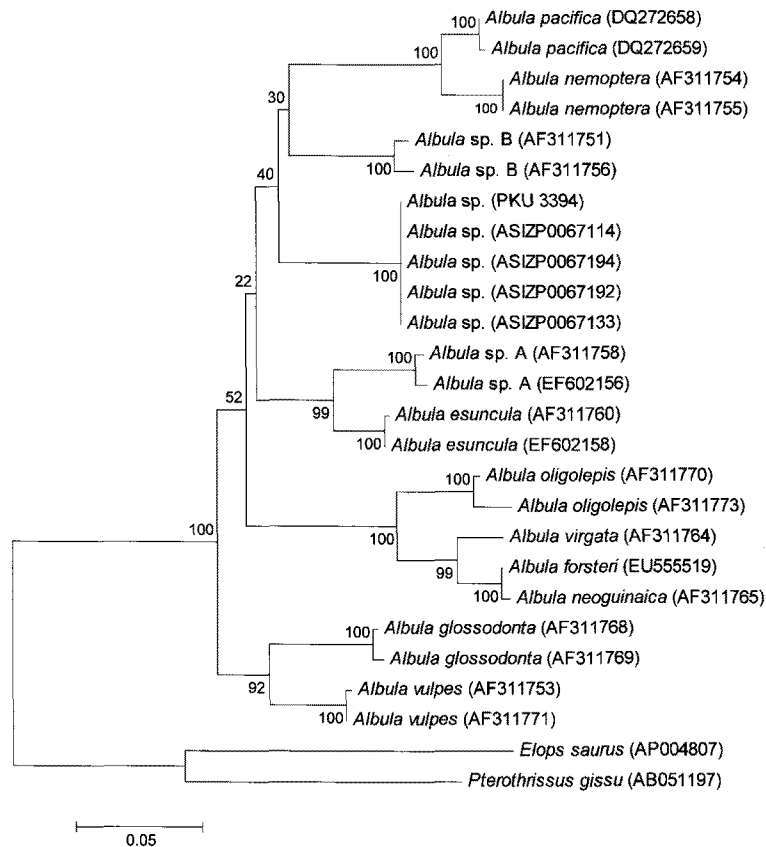


Figure 4. NJ-tree showing relationships among *Albula* species including *Albula* sp. Numbers at branches indicate bootstrap probabilities in 1000 bootstrap replications. Bar indicates genetic distance of 0.05.

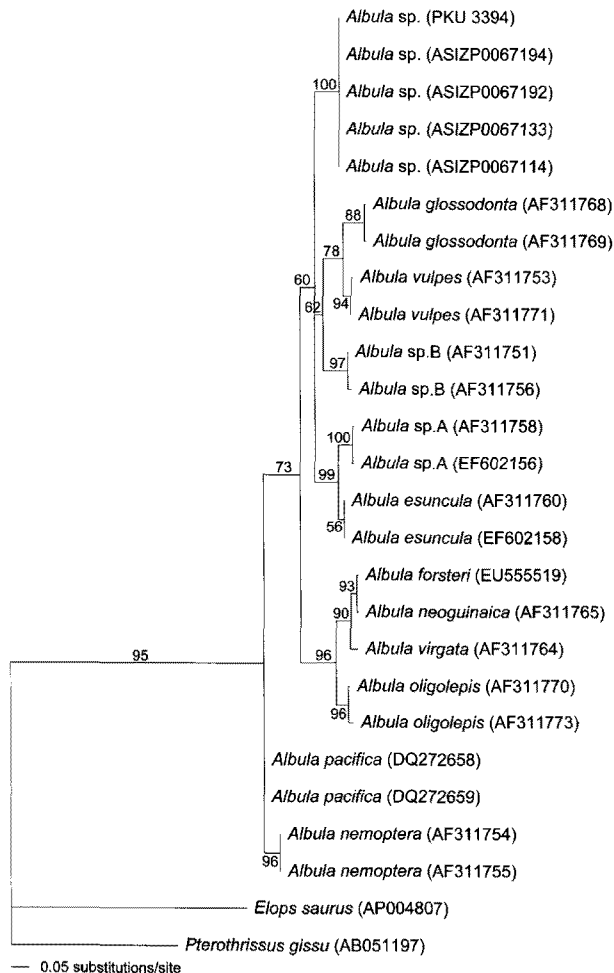


Figure 5. ML-tree showing relationships among *Albula* species including *Albula* sp. Numbers at branches indicate bootstrap probabilities in 100 bootstrap replications. Bar indicates substitutions/site of 0.05.

et al. (2005). The scientific names of these species are inappropriate according to this molecular analysis, showing that the species of *Albula* have been taxonomically confused.

In morphology, one Korean *Albula* specimen corresponded to the four Taiwan *Albula* specimens in the following morphological diagnostic characters suggested by Hidaka et al. (2008); the number of vertebrae 77–78, lower jaw pointed, and posterior tip of pelvic fin reaching to anterior margin of anus. Therefore, we regarded five specimens of *Albula* sp. to be same species because of their identical morphological features.

Albula sp. is very similar to *A. argentea* sensu Hidaka et al. (2008) in having a pelvic fin that extends to the anterior margin of the anus (Figure 3), but it is distinguishable by its numbers of anal fin rays (nine in *Albula* sp. vs. eight in *A. argentea*), pored lateral-line scales (77–80 vs. 68–74, respectively) and vertebrae (77–78 vs. 71–74, respectively; Table 2). In its body

measurements, *Albula* sp. also differs from *A. argentea* in the percentage caudal peduncle depth (6.7%–7.3% SL in *Albula* sp. vs. 7.0%–9.0% SL in *A. argentea*; Table 2). *Albula* sp. is distinguishable from *A. glossodonta* by the shape of its lower jaw (lower jaw pointed in *Albula* sp. vs. rounded in *A. glossodonta*), the number of vertebrae (77–78 vs. 67–69, respectively), and the number of pored lateral-line scales (77–80 vs. 66–70, respectively; Table 2). *Albula* sp. is also distinguishable from *A. oligolepis* and *A. virgata* by its number of vertebrae (77–78 in *Albula* sp. vs. 64–66 in *A. oligolepis* and 65–68 in *A. virgata*) and pored lateral-line scales (77–80 vs. 61–65 and 63–67, respectively; Table 2).

As a result of above, we believe that *Albula* sp. may be an undescribed species from the Indo-Pacific. However, further research, such as comparing type specimens of the other congeneric species, is needed for clarifying their taxonomic status confidently.

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References

- Aizawa M. 2000. Albulidae. In: Nakabo T, editor. Fishes of Japan with pictorial keys to the species. 2nd ed. Tokyo: Tokai University Press. p. 189, 1450.
- Beebe W. 1942. Eastern Pacific expeditions of the New York zoological society. XXX. Atlantic and Pacific fishes of the genus *Dixonina*. Zoologica. 27:43–48.
- Bloch ME, Schneider JG. 1801. Systema Ichthyologiae iconibus cx Illustratum. Post obitum auctoris opus inchoatum absolvit, corxit, interpolavit Jo. Gottlob Schneider, Saxo. Berolini.
- Bowen BW, Karl SA, Pfeiler E. 2008. Resolving evolutionary lineages and taxonomy of bonefishes (*Albula* spp.). In: Ault JS, editor. Biology and management of the world tarpon and bonefish fisheries. Boca Raton (FL): CRC Press. p. 147–154.
- Colborn J, Crabtree RE, Shaklee JB, Pfeiler E, Bowen BW. 2001. The evolutionary enigma of bonefishes (*Albula* spp.): cryptic species and ancient separations in a globally distributed shorefish. Evolution. 55:807–820.
- Cuvier G, Valenciennes A. 1847. Histoire naturelle des poissons. Tome dix-neuvième. Strasbourg: Imprimerie de V. Berger-Levrault.
- Forsskål P. 1775. Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit. Post mortem auctoris edidit Carsten Niebuhr. Hauniæ.
- Fowler HW. 1911. A new albuloid fish from Santa Domingo. Proc Acad Nat Sci Phila. 62:651–654.
- Garmin S. 1899. Reports on an exploration off the west coasts of Mexico, central and south America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. fish commission steamer “Albatross” during

- 1891, Lieut. Commander Z.L. Tanner, U.S.N., commanding. XXVI. The fishes. Mem Mus Comp Zool. 24:1–431.
- Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucl Acids Symp Ser. 41:95–98.
- Hidaka K, Kishimoto H, Iwatsuki Y. 2004. A record of an albulid fish, *Albula glossodonta*, from Japan (Albuliformes: Albulidae). Japan J Ichthyol. 51:61–66.
- Hidaka K, Iwatsuki Y, Randall JE. 2008. A review of the Indo-Pacific bonefishes of the *Albula argentea* complex, with a description of a new species. Ichthyol Res. 55:53–64.
- Hildebrand SF. 1963. Family Albulidae. In: Bigelow HB, Bradbury MG, Dymond JR, Greeley JR, Hildebrand SF, Mead GW, Miller RR, Rivas LR, Schroeder WC, Suttkus RD, Vladykov VD, editors. Fishes of the western North Atlantic. New Haven (CT): Sears Foundation for Marine Research, Yale University. p. 132–147.
- Hubbs CL, Lagler KF. 2004. Fishes of the Great Lakes Region. Rev. ed. Ann Arbor: The University of Michigan Press. p. 1–276.
- Jordan DS, Jordan EK. 1922. A list of the fishes of Hawaii, with notes and descriptions of new species. Mem Carnegie Mus. 10:1–92.
- Kim IS, Choi Y, Lee CL, Lee YJ, Kim BJ, Kim JH. 2005. Illustrated book of Korean fishes. Seoul: Kyohak-Publishing. p. 1–615.
- Kim BJ, Kim S, Seo HS, Oh J. 2008. Identification of *Albula* sp. (Albulidae: Albuliformes) leptocephalus collected from the southern coastal waters of Korea using cytochrome *b* DNA sequences. Ocean Sci J. 43:101–106.
- Kimura M. 1980. A Simple Method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. J Mol Evol. 16:111–120.
- Linnaeus C. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decimal, reformata. Holmiæ.
- Matsubara K. 1955. Fish morphology and hierarchy Part I. Tokyo: Ishizaki-Shoten. p. 1–789.
- Mori T. 1952. Check list of the fishes of Korea. Mem Hyogo Univ Agri. 1:1–228.
- Nelson JS. 2006. Fishes of the world. 4th ed. Hoboken (NJ): Wiley. p. 1–601.
- Pfeiler E. 2008. Resurrection of the name *Albula pacifica* (Beebe, 1942) for the shafted bonefish (Albuliformes: Albulidae) from the eastern Pacific. Rev Biol Trop. 56:839–844.
- Pfeiler E, Bitler BG, Ulloa R. 2006. Phylogenetic relationships of the Shafted Bonefish *Albula nemoptera* (Albuliformes: Albulidae) from the eastern Pacific based on cytochrome *b* sequence analyses. Copeia. 2006:778–784.
- Pfeiler E, Bitler BG, Ulloa R, van der Heiden AM, Hastings PA. 2008. Molecular identification of the Bonefish *Albula esuncula* (Albuliformes: Albulidae) from the tropical eastern Pacific, with comments on distribution and morphology. Copeia. 2008:763–770.
- Posada D, Buckley TR. 2004. Model selection and model averaging in phylogenetics: advantages of akaike information criterion and bayesian approaches over likelihood ratio tests. Syst Biol. 53:793–808.
- Posada D, Crandall KA. 1998. MODELTEST: testing the model of DNA substitution. Bioinformatics. 14:817–818.
- Randall JE. 2005. Reef and shore fishes of the south Pacific, New Caledonia to Tahiti and the Pitcairn Islands. Honolulu: University of Hawaii Press. p. 1–707.
- Rivas LR, Warlen SM. 1967. Systematics and biology of the bonefish, *Albula nemoptera* (Fowler). Fish Bull. 66:251–258.
- Scopoli JA. 1777. Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, characteribus essentialibus donata, in tribus divisa, subinde ad leges naturae. Pragae.
- Shen SC, Lee SC, Shao KT, Mao HC, Chen CH, Chen CC, Tzeng CS. 1993. Fishes of Taiwan. Taipei: National Taiwan University. p. 1–960.
- Smith DG. 2002. Albulidae. In: Carpenter KE, editor. The living marine resources of the western central Atlantic. Vol. 2, Bony fishes part 1 (Acipenseridae to Grammatidae). Rome: Food and Agricultural Organization. p. 683–684.
- Swofford DL. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), version 4.0b10. Sunderland: Sinauer Associates. p. 1–142. Available from: <http://paup.csit.fsu.edu/> (accessed 5 Sep 2010).
- Tamura K, Dudley J, Nei M, Kumar S. 2007. MEGA4: Molecular Evolutionary Genetic Analysis (MEGA) Software Version 4.0. Mol Biol Evol. 24: 1596–1599. Available from: http://kumarlab.net/pdf_new/TamuraKumar07.pdf/ (accessed 5 Sep 2010).
- Zhang Q. 1984. Elopiformes. In: Chu YT, editor, editor. The fishes of Fujian Province. Fujian: Fujian Science and Technology Press. p. 107–112.