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Identification of the Commercially Important Oreosomatid Fish (Zeiformes: Teleostei) of the Emperor Seamounts, with Comments on Diagnostic Characters of the Species

Koichi Hoshino[1,6], Kunpei Kosaka[2], Kota Sawada[3,4], and Masashi Kiyota[3,5]

[1] *Fisheries Technology Institute, Japan Fisheries Research and Education Agency, 1551-8 Taira-machi, Nagasaki 851-2213, Japan*
E-mail: hoshinok@affrc.go.jp
[2] *Tokyo University of Marine Science and Technology, 4-5-7 Kohnan, Minato-ku, Tokyo 108-8477, Japan*
[3] *National Research Institute of Far Seas Fisheries, Japan Fisheries Research and Education Agency, 2-12-4 Fukuura, Kanazawa-ku, Yokohama, Kanagawa 236-8648, Japan*
[4] *Present Address: Fisheries Resources Institute, Japan Fisheries Research and Education Agency, 2-12-4 Fukuura, Kanazawa-ku, Yokohama, Kanagawa 236-8648, Japan*
[5] *Present Address: Graduate School of Fisheries and Environmental Sciences, Nagasaki University, 1-14 Bunkyo-machi, Nagasaki 852-8521, Japan*
[6] *Corresponding author*

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An oreosomatid of the genus *Allocyttus* McCulloch, 1914 is fished commercially on the Emperor Seamounts. However, the species' identity is uncertain, as is the taxonomy of the oreosomatid species of the seas around Japan, where the names *Allocyttus verrucosus* Gilchrist, 1906 (type locality: off South Africa) and *A. folletti* Myers, 1960 (type locality: off California) have both been used. From its anticipated susceptibility to over-exploitation, it is urgent to establish the correct taxonomic identity to facilitate effective management measures. Meristics, morphometrics and scale characters of the specimens from the Emperor Seamounts and Japan agreed well with data of the holotype of *A. folletti* and differed from those of *A. verrucosus*, confirming that those specimens represent *A. folletti*. Oreosomatids reported from the western North Pacific in the literature were identified as *A. folletti*. From the data of the present study and historical references, *A. folletti* is thought to be distinguished from *A. verrucosus* by the following characters: more dorsal- and anal- spines+rays (36–42 vs. 33–38 and 31–35 vs. 27–33 respectively), more total vertebrae (37–41 vs. 34–38), greater numbers of enlarged scales of dorsal- (S-DFB) and anal-fin base (S-AFB) (31–42 vs. 26–31, and 29–37 vs. 25–28 respectively), more spines on the margin of S-DFB and S-AFB (up to 7–12 vs. 3–6), a shorter preanal-fin length (53.8–63.6% vs. 64.8–83.7% of SL), a longer caudal peduncle (10.4–15.6% vs. 6.1–10.2% of SL), a shorter head (32.9–40.4% vs. 38.5–48.4% of SL), and cycloid scales on the mid-side of body (vs. ctenoid). Available data indicate that *A. folletti* reaches up to 537 mm SL, larger than *A. verrucosus* (up to ca. 325 mm SL). From the anticipated slow growth and longevity, concern is raised regarding the susceptibility of *A. folletti* to over-exploitation.

Key Words: *Allocyttus folletti*, *Allocyttus verrucosus*, Oreosomatidae, northwestern Pacific.

Introduction

Members of the genus *Allocyttus* McCulloch, 1914 of the family Oreosomatidae (Zeiformes), commonly known as "oreos," are deep-sea benthopelagic (Karrer 1986a, b; Heemstra 2016) fishes widely distributed in the waters of seamounts and continental slopes of the Pacific, Atlantic and Indian Oceans (James et al. 1988). The monophyly of the Oreosomatidae is demonstrated by the phylogenetic studies (Tyler et al. 2003; Tyler and Santini 2005; Grande et al. 2018). Within the family, *Allocyttus* is characterized by having a deep and compressed body, a large eye (but its diameter 52% or less of head length), the first dorsal-fin spine shorter than the second, and the predorsal profile nearly straight without an abrupt rise anterior to the dorsal fin (James et al. 1988). The juveniles are pelagic, and significantly morphologically distinct from the adults in having a swollen abdomen with two rows of cone-like scutes, which are reduced but may remain in adults as patches of enlarged scales between the pectoral and pelvic fins (Kobayashi et al. 1968; Hart 1973; James et al. 1988).

Four species are recognized in the genus: *Allocyttus verrucosus* (Gilchrist, 1906), *A. folletti* Myers, 1960, *A. guineensis* Trunov and Kukuev, 1982, and *A. niger* James, Inada, and Nakamura, 1988. *Allocyttus niger* is distributed in the South West Atlantic and Southern Indian Oceans, and off Southern Australia and New Zealand (Heemstra 2016). It is easily distinguished from its congeners by the presence of numerous minute spinules on the dorsal- and anal-fin rays, strongly adherent ctenoid scales in adults and strong dorsal- and anal-fin spines (James et al. 1988). *Allocyttus guineensis* from the southeastern Atlantic coast of Africa from Mauritania to Angola (Heemstra 2016) differs from congeners in the combination of strongly adherent cycloid scales and relatively weak dorsal- and anal-fin spines (Trunov 1982). Although the documented distributions of *A. folletti* and *A. verrucosus* have been confused due to incorrect identifications, the former has been reported from the North Pacific (e.g., Myers 1960; Mecklenburg et al. 2002; present study) while the latter is currently thought to occur in the temperate waters of the North Atlantic and circumglobally in the Southern Hemisphere (e.g., Bray 2015; present study). Myers (1960) noted that *A. folletti* differs from *A. verrucosus* in having somewhat deciduous cycloid scales on the entire mid-lateral side area, lateral line and caudal peduncle, as well as more subtle features [more concave predorsal profile, flatter belly, less smoothly rounded snout, and more prominent and more rugose nasal boss (=bony projection)]. He also noted that none of the three type specimens of *A. folletti* from the coast of California had any trace of abdominal scutes, unlike in *A. verrucosus*.

Many oreo species are commercially important, including the one (Fig. 1A) exploited by boats fishing on the Emperor Seamounts, a volcanic seamounts chain extending from the western end of the Hawaiian Ridge (30°N, 175°E) to the Aleutian Trench (53°N, 164°E) in the western North Pacific (Nishida et al. 2016). However, the taxonomic identity of this species has been uncertain, due in part to confusion surrounding the taxonomy of the oreosomatid species known from the seas around Japan. Abe and Hotta (1962) reported and described a single oreosomatid specimen (181 mm SL) captured off Kinkazan, Miyagi Prefecture, Japan, and identified it as *Allocyttus verrucosus* rather than *A. folletti*, mainly because the specimen had two rows of scutes between the pectoral fin and preanal contour. Kobayashi et al. (1968) reported an "immature" specimen (268 mm SL) from the north-western Bering Sea and two "young" specimens (both 78 mm SL) from the central northern Pacific, and documented all three as *A. verrucosus*. They considered *A. folletti* a junior synonym of *A. verrucosus*, ascribing the distinguishing characters proposed by Myers (1960) to ontogenetic change or individual variance. Maruyama (1970) described a specimen from off Erimo (Pacific coast of Hokkaido, Japan) as *A. verrucosus*. Kido (1983) described a specimen (292 mm SL, but the picture represents a different specimen of 431 mm SL) from off north-eastern Japan as *A. verrucosus* based on the two rows of scutes between the pectoral and pelvic fins.

In a revision of the oreosomatid fishes from the southern oceans, James et al. (1988) discussed that the records of *A. verrucosus* from the North Pacific (Welander et al. 1957; Abe and Hotta 1962; Kobayashi et al. 1968; Hughes 1981), as well as *A. folletti* in Myers (1960), represent a different taxon or taxa from *A. verrucosus* of the southern oceans (Fig. 1B) noting that "scale structure, scute patterns, and meristic counts … together with the geographic separation suggest strongly that the northern and southern Pacific forms are not conspecific." However, James et al. (1988) did not adequately demonstrate how *A. verrucosus* and the North Pacific oreosomatid differ, and thus their comments were largely overlooked by subsequent researchers. Thereafter, the name *A. verrucosus* has been applied to the oreosomatid from the western North Pacific by many authors, mainly from Japan (Ida et al. 1992; Nakabo 1993, 2000, 2002; Amaoka et al. 1995, 2011; Inada 1997; Sheiko and Fedorov 2000; Maeda and Tsutsui 2003; Tokranov et al. 2004). One notable exception was Mecklenburg et al. (2002), who recorded the range of *A. folletti* as including the Bering Sea and the Pacific Ocean from central California to Honshu, Japan, and briefly noted that *A. verrucosus* of the South Pacific differed by having fewer fin elements and vertebrae, more cones (=scutes) in the upper abdominal row, and larger spots on the prejuvenile. Nakabo and Kai (2013) applied the name *A. folletti* to the oreosomatid of the western North Pacific, citing the discussion of James et al. (1988) and Mecklenburg et al. (2002),

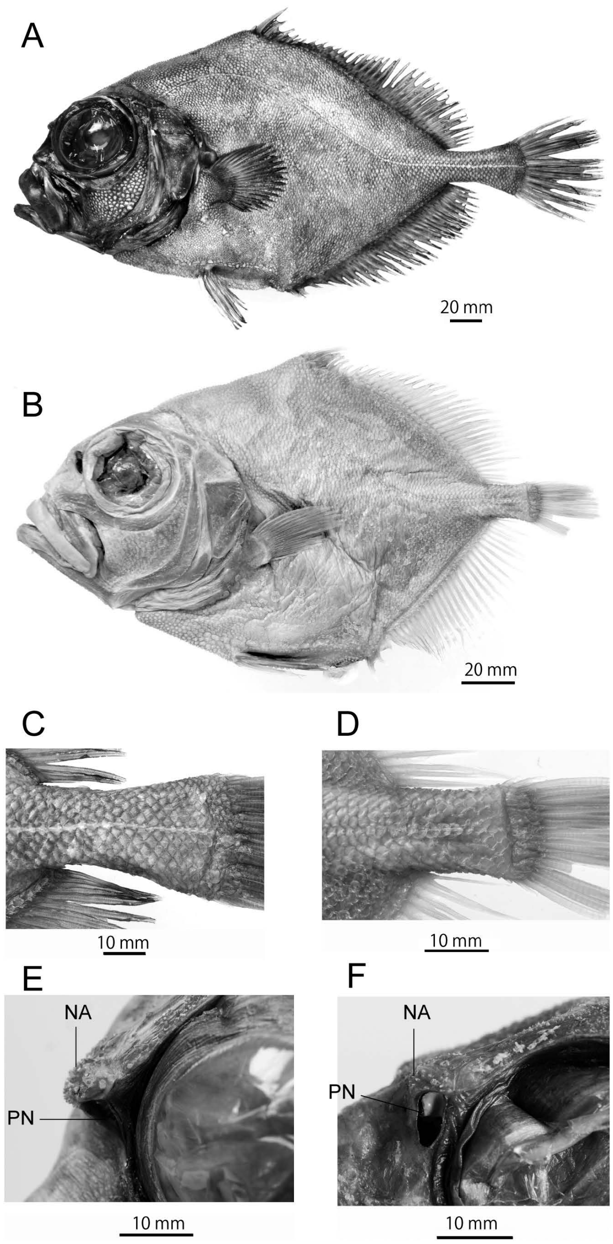

Fig. 1. Lateral view of oreosomatids. A, *Allocyttus folletti* from the Emperor Seamounts, SNFR 22402, 289.8 mm SL; B, *Allocyttus verrucosus* from New Zealand, NSMT-P 41168, 187.2 mm SL; caudal peduncle of *A. folletti*; C, SNFR 10560, 293.4 mm SL, Emperor Seamounts, and that of *A. verrucosus*; D, NSMT-P 41168, 187.2 mm SL, New Zealand; nasal of oreosomatids; E, *A. folletti*, SNFR 10561, 347 mm SL, Emperor Seamounts; F, *A. verrucosus*, NSMT-P 113107, 238.4 mm SL, west coast of Australia. Abbreviations: NA, nasal; PN, posterior nostril.

but did not document the differences between *A. folletti* and *A. verrucosus*. Mundy (2005) regarded the oreosomatid previously reported from the Emperor Seamounts (e.g., Borets 1986) as *A. folletti* without discussion.

At present, the differences between *A. folletti* and *A. verrucosus* are not well understood. For example, the presence or absence of two rows of scutes on the side of body between the pectoral and pelvic fins was considered as a valid character to distinguish *A. verrucosus* (present) from *A. folletti* (absent) (e.g., Myers 1960; Abe and Hotta 1962; Kido 1983). However, the scutes are illustrated in the figures of *A. folletti* in Mecklenburg et al. (2002), and the presence of the scutes was listed as a diagnostic character of *A. folletti* by Nakabo and Kai (2013), without discussion regarding the disagreement this posed with preceding studies (e.g., Myers 1960; Abe and Hotta 1962; Kido 1983). Ward et al. (1996) listed characters to distinguish the two species that had not been previously documented (number of pectoral-fin rays and lachrymal width) but they were not cited in the subsequent studies providing morphological data of *A. folletti* (e.g., Mecklenburg et al. 2002).

Uncertainty in the identity and applicable scientific name of the oreosomatid from the Emperor Seamounts will undermine the quality of future stock management, which is an international responsibility under the North Pacific Fisheries Commission (NPFC) (Nishida et al. 2016). This species is expected to be susceptible to over-exploitation (see Discussion), and the needs are therefore urgent to determine its scientific name and implement effective management measures.

The major goal of this study is to establish the taxonomic identity of the oreosomatid from the Emperor Seamounts, thereby contributing to appropriate stock management, and to provide reliable diagnostic characters to distinguish *A. folletti* from *A. verrucosus*.

Materials and Methods

The left-hand side of each specimen was examined except when damaged or in an abnormal condition. Methods of counts and measurements mostly follow James et al. (1988), with some modifications. For standard length (SL), head length (HL), predorsal-fin length (PDFL), and preanal-fin length (PAFL), both the ordinary measurement from the snout tip (abbreviated as SL1, HL1, PDFL1 and PAFL1 respectively), and a modified measurement from the anterior tip of maxillary (SL2, HL2, PDFL2 and PAFL2 respectively), were made. The latter is thought to provide a more accurate basis for comparative proportions because it eliminates the influence of any mouth protrusion, but the former measurements are needed for comparisons with the literature. SL2 and HL2 correspond to Myers' (1960) "standard length minus premaxillary" and "head length minus premaxillary" respectively. The mouth, if protruding, was retracted to its natural closed position when possible; if not, the specimen was excluded for measurements from the snout tip to preclude any biased values. For body depth (BD), BD1 is the greatest vertical dimension of body at the dorsal-fin origin (as in James et al. 1988), and BD2 is the distance from the dorsal-fin origin to the anal-fin origin (as in Myers 1960). Abdominal edge length (AEL) and thoracic edge length (TEL) follow Myers (1960). P2O-AFO is the length between the pelvic-fin origin and the anal-fin origin [=thoracic edge length of James et al. (1988)]. For caudal-peduncle length (CPL), CPL1 is the distance from the anal-fin insertion to the middle of the caudal-fin base; CPL2 is the distance from the anal-fin insertion to the exposed origin of the first ventral procurrent ray (as in Yearsley and Last 1998). Depth of caudal-fin base is the depth of the caudal-fin base between the exposed origins of the first procurrent rays of the upper and lower lobes. Lachrymal width (LW) is the minimum dorsoventral dimension of part of lachrymal below eye (posterior to the articulation with the lateral ethmoid) (Ward et al. 1996; G. K. Yearsley, pers. comm.). S-DFB and S-AFR are the serial enlarged scales at the dorsal- and anal-fin bases respectively. Vertebrae were examined by radiography. The vertebrae, S-DFB, S-AFB and the spines on S-DFB and S-AFB of the holotype of *A. folletti* (CAS-SU 15377) were counted from the digital images downloaded from "Ichthyology Primary Types Imagebase" of California Academy of Sciences (https://www.calacademy.org/scientists/ichthyology-primary-types-imagebase). Institutional acronyms follow Fricke and Eschmeyer (2019).

Comparative material examined. *Allocyttus folletti*. 2 specimens, Japan. NSMT-P 30689 (n=1), 194.7 mm SL, Suruga Bay, Shizuoka Prefecture, 34°50′N, 138°35′E, July–August 1969; HUMZ 72625 (n=1), 287.1 mm SL, off Fukushima Prefecture, 37°30.0′N, 142°19.5′E, 815–860 m deep, 24 January 1978, trawl. *Allocyttus verrucosus*. 7 specimens. NSMT-P 41168 (n=1), 187.2 mm SL, New Zealand, date unknown, R/V Shinkai-maru; NSMT-P 112857 (n=1), 201.5 mm SL, West coast of Australia, date unknown, R/V Kaiyo-maru; NSMT-P 112858, 110.2 mm SL, West coast of Australia, date unknown, R/V Kaiyo-maru; NSMT-P 113107 (n=1), 238.4 mm SL, West coast of Australia, 31°39.3′S, 114°44.0′E, 1035 m deep, 15 November 1975, R/V Kaiyo-maru. BSKU 48476–48478 (n=3), 121.4–151.3 mm SL, off South Africa, 34°26.6′S, 26°00.8′E, 750 m, 3 June 1990, bottom trawl.

Results

***Allocyttus folletti* Myers, 1960**

(Figs 1A, C, E, 2A, C, 3)

Allocyttus verrucosus (non Gilchrist, 1906): Welander et al. 1957: 245–246 (description; off North Pacific); Abe and Hotta 1962: 152–156, figs 1–8 (description; off Kinkazan, Japan); Kobayashi et al. 1968: 1–5, pl. I (description; western Bering Sea and western North Pacific); Maruyama 1970: 52–54, fig. 9 (description; off Erimo, Japan); Maruyama 1971: 33, fig. 36 (list; off Erimo, Japan); Kido 1983: 126–127, 203, fig. (description: Japan); Machida 1984: 118, pl. 103-A (description; Japan); Ida et al. 1992: 86, fig. (description; off Iwate Pref., Japan); Nakabo 1993:

467, 3 figs (pictorial key); Amaoka et al. 1995: 127, fig. (description; Hokkaido, Japan); Inada 1997: 168, fig. (note on distribution; off Kushiro, Japan); Nakabo 2000: 508, 3 figs. (pictorial key); Nakabo 2002: 508, 3 figs (pictorial key); Tokranov et al. 2004: 210–212, figs 1–3 (distribution, length-weight relationship; Northern Kurile Islands and Southeast Kamchatka); Kitagawa et al. 2008: 50, fig. (diagnosis; Japan); Amaoka et al. 2011: 168, fig. (description; Hokkaido, Japan).

Allocyttus folletti Myers, 1960: 89–98, fig. 1 (original description; type locality: California); Miller and Lea 1972: 84–85, fig. (diagnosis); Anderson et al. 1979: 262 (meristics; California); Eschmeyer and Herald 1983: 126, pl. 48, fig. 18 (diagnosis); Nagtegaal 1983: 89, fig. 1 (description; British Columbia); Cook and Long 1985: 57 (occurrence; Bering Sea); Gillespie and Saunders 1994: 348 (description; British Columbia); Ward et al. 1996: 41 (diagnosis); Mecklenburg et al. 2002: 327–329, 2 figs (diagnosis; Alaska); Nakabo and Kai 2013: 601, 1902, 3 figs (pictorial key, taxonomic note); Kamikawa 2017: 176, fig. (description; West Coast of U. S. A.); Amaoka et al. 2020: 207, figs (description; Hokkaido, Japan).

Allocyttus sp.: Hart 1973; 266–267, fig. (description of juvenile; mid-Pacific, west of British Columbia).

Material examined. *Emperor Seamounts*—21 specimens. SNFR 10560 (n=1), 293.4 mm SL, Koko Seamount, 35°39′N, 171°03′E to 35°38′N, 171°03′E, 361–355 m deep, 24 July 2007, F/V Tomi-maru No. 58; SNFR 10561 (n=4), 301–347 mm SL, collected with SNFR 10560; SNFR 11127 (n=1), 279.4 mm SL, Kinmei Seamount, 33°40.0′N, 172°00.0′E, 600 m, 13 May 1994; SNFR 18692 (n=1), 537 mm SL, Kinmei Seamount, 33°46′N, 171°54′E, 850–893 m, 27 September 2012, F/V Shoshin-maru No. 88; SNFR 22400–22408 (n=9), 269.3–300.8 mm SL, Yuryaku Seamount, 32°19.16′N, 172°19.25′E to 32°40.63′N, 172°13.09′E, 486–670 m, 5 February 2019, F/V Kaiyo-maru No. 38; NSMT-P 72807 (n=1), 337 mm SL, Colahan Seamount, 31°01′N, 175°54′E to 31°02′N, 175°52′E, 285 m, 17 September 2005, F/V. Yokei-maru No. 5; FAKU72487 (n=1), 328 mm SL, Kinmei Seamount, 33°40′N, 172°00′E, 600 m, 13 May 1994; FAKU72575 (n=1), 397 mm SL, collected with FAKU72487; FAKU119906 (n=1), 321 mm SL, Hancock Seamounts, 3 March 1973, R/V Kaiyo-maru; FAKU119907 (n=1), 382 mm SL, collected with FAKU119906.

Description. Meristics are presented in Table 1, and morphometrics as % of SL1 and SL2 are presented in Tables 2 and 3 respectively. Body oval, laterally compressed and deep; deepest at dorsal-fin origin, its depth greater than head length. Predorsal profile usually slightly convex (but sometimes straight) from dorsal-fin origin to vertical through uppermost end of gill opening, slightly concave or straight in front of same vertical. Snout profile steep. Thorax flat ventrally. Midline of abdomen gently keeled between pelvic-fin origin and anus (abdominal edge). Caudal peduncle slender, deeper posteriorly (Fig. 1C), deepest at caudal-fin base.

Head large, 34.6–39.3% of SL1. Eye large, 12.5–18.4% of SL1. Mouth large, oblique, greatly extensible. Maxillary ex-

Table 1. Meristics of *Allocyttus folletti* and *A. verrucosus*.

Characters	*A. folletti*			*A. verrucosus*	
	Emperor Seamounts N=21	Japan N=2	Myers (1960)[1] +holotype image N=3	Examined specimens N=7	Gilchrist (1906) N=1?
DS	6–7	6	7 (5–7)	6	6
DR	30–33	32	32 (30–33)	28–30	31
DS+DR	37–40	38	39 (37–39)	34–36	37
AS	2–4	2–3	3 (3)	2–3	3
AR	29–32	30–31	31 (31–32)	27–29	29
AS+AR	32–35	32–34	34 (34–35)	29–31	32
P1R	19–21	19–21	21 (19–21)	17–20	—
P2S	1	1	1 (1)	1	—
P2R	6	6	6 (6)	6	—
LLS	82–93	88–90	95 (85–95)	82–92	95
UGR	3–6	4–6	6 (6–7)	3–6	—
LGR	16–22	19–20	19 (19–25)	18–19	—
TGR	20–27	23–26	25 (25–32)	21–24	—
AV	12–13	12–13	*12*	12–13	—
CV	24–27	27–28	*28*	23–25	—
TV	37–40	40	*40*	35–37	—
S-DFB	31–42	32–33	*33*	26–31	—
S-AFB	29–37	29–31	*29*	25–28	—

Abbreviations: AR, anal-fin rays; AS, anal-fin spines; AV, abdominal vertebrae; CV, caudal vertebrae; DR, dorsal-fin rays; DS, dorsal-fin spines; LGR, gill rakers of lower limb; LLS, lateral-line scales; P1R, pectoral-fin rays; P2R, pelvic-fin rays; P2S, pelvic-fin spine; S-AFB, enlarged scales of anal-fin base; S-DFB, enlarged scales of dorsal-fin base; TGR, total gill rakers; TV, total vertebrae; UGR, gill rakers of upper limb. [1] Data of the holotype, followed by the range of holotype+two paratypes in parentheses. Digits in italics were counted from the digital images of the holotype (CAS-SU 15377).

Table 2. Morphometrics as % of SL1 (snout tip to middle of caudal-fin base) of *Allocyttus folletti and A. verrucosus*.

Characters	*A. folletti*			*A. verrucosus*	
	Emperor Seamounts N=21	Japan N=1	Myers (1960)[1] N=3	Examined specimens N=7	Gilchrist (1906)
SL1 (mm)	269.3–537	287.1	347 (162–347)	110.2–238.4	?
HL1	34.6–39.3	34.6	36.3 (36.3–42.0)	40.2–43.1	*41.5*
PDFL1	50.2–57.6	53.5	51.0 (51.0–58.0)	53.0–62.3	*60.8*
PAFL1	53.8–62.4	55.5	62.8 (62.8–63.6)	66.5–82.0	*64.5*
BD1	50.4–55.9	53.3	*51.3* (—)	56.9–68.7	*64.1*
BD2	51.5–57.5	53.7	53.3 (53.3–58.6)	57.0–65.7	*65.2*
DFBL	42.8–50.9	47.7	49.3 (46.0–49.3)	43.9–48.1	*48.7*
AFBL	38.8–43.1	43.8	40.1 (37.8–42.0)	36.8–40.5	*41.4*
HW	18.7–22.3	19.8	—	19.8–23.3	—
UJL	14.0–17.0	15.2	15.9 (15.4–17.9)	14.7–19.2	*18.3*
LJL	19.8–22.7	21.5	19.6 (19.6–23.5)	22.1–24.4	*23.5*
ED	12.5–18.4	16.3	*14.2* (—)	15.1–19.0	*18.4*
SNL	8.5–13.6	9.6	10.1 (10.1–12.4)	10.3–13.5	*13.0*
LW	1.7–2.5	2.1	*2.0*	2.5–3.6	*4.2*
P1L	14.5–17.6	15.3	16.4 (15.4–19.1)	16.1–19.9	*18.4*
P2L	14.2–19.3	17.1	—	19.0–24.4	*19.1*
DS2L	8.4–11.0	10.2	8.2 (8.2–11.7)	7.4–11.6	*7.9*
DRL	11.6–14.7	13.0	11.8 (10.8–13.6)	14.6–17.3	*18.2*
AS1L	5.2–7.6	—	—	5.9–6.9	*6.4*
ARL	13.9–15.5	14.0	13.3 (12.7–16.1)	15.5–18.3	*18.5*
P2SL	12.9–16.0	15.2	13.0 (13.0–22.2)	11.0–16.7	—
TEL	14.6–18.5	16.6	17.3 (17.3–18.5)	20.6–24.9	—
AEL	14.6–20.2	18.2	18.4 (18.4–19.7)	20.1–26.0	—
P2O-AFO	17.7–23.1	20.5	—	23.9–29.6	—
CPL1	11.2–14.8	14.6	*13.5* (—)	7.7–10.2	*11.9*
CPL2	10.4–13.0	13.8	—	6.1–8.9	—
CPD	5.0–6.7	6.3	5.8 (5.8–6.2)	5.9–6.9	*7.0*

Abbreviations: AEL, abdominal edge length; AFBL, anal-fin base length; ARL, longest anal-fin ray length; AS1L, 1st anal-fin spine length; BD1, body depth 1; BD2, body depth 2; CPD, caudal-peduncle depth; CPL1, caudal peduncle length 1; CPL2, caudal-peduncle length 2; DFBL, dorsal-fin base length; DRL, longest dorsal-fin ray length; DS2L, 2nd dorsal-fin spine length; ED, eye diameter; HL1, head length 1; HW, head width; LJL, lower-jaw length; LW, lachrymal width; P1L, pectoral-fin length; P2L, pelvic-fin length; P2SL, pelvic-fin spine length; PAFL1, pre-anal fin length 1; PDFL1, pre-dorsal fin length 1; P2O-AFO, length from pelvic-fin origin to anal-fin origin; SNL, snout length; TEL, thoracic edge length. For methods of measurement, refer to text. [1] Data of holotype, and range of holotype+two paratypes in parentheses. Digits in italics indicate measurement from figure of original description.

tending posteriorly nearly to below middle of eye when mouth closed. Opercular bones with radiated bony striations, scaleless, except opercle sparsely scaled. Numerous spinules on all exposed bones on head. Nasal projected anteriorly above anterior nostril, with enlarged spinules (more prominent in larger specimens). Nostrils close together: anterior one circular, oriented anteriorly; posterior one vertically elongate, oriented laterally, immediately anterior to eye. Nasal projected forward above posterior nostril (Fig. 1E). Lower surface of dentary with numerous spinules and longitudinal striations. Teeth on both jaws minute, conical, slightly curved inward, in irregular 1–3 rows. Vomerine teeth similar to jaw teeth in shape, size and arrangement. Palatine teeth absent.

Dorsal-, anal-, and pelvic-fin spines robust, densely striated; first dorsal-fin spine about one-third of second spine in length. First anal-fin spine longer than second and third spines. All dorsal-, anal- and pectoral-fin soft rays simple, densely segmented. Spinous and soft-ray portions of anal fin continuous, with low membrane. Pectoral fin small, rounded, posterior margin falling slightly short of vertical through anal-fin origin. Pelvic fin reaching or extending slightly beyond anus when depressed, its spine reaching or falling slightly short of anus. Caudal fin rounded.

Lateral line gently arched, nearly parallel to dorsal contour in anterior two-thirds, posterior third straight. Scales mostly cycloid and deciduous mid-laterally (Fig. 2A), and on caudal peduncle, basal part of caudal fin and lateral line; thickened cycloid or ctenoid with a few spinules on lower side of thorax and abdomen; thickened ctenoid with prominently enlarged and elevated spinules at nape and ventral surface of thorax and abdomen; those on ventral midline of abdomen especially thickened and enlarged in large specimens; row of enlarged scales along base of dorsal and anal fins (S-DFB and S-AFB respectively) forming sheath of scales, with up to 7–12 (margin) and 1–3 (center) elevated spines per scale (Fig. 2C). Single row of smaller scales with 1–3 spinules along medial side of S-DFB and S-AFB. Two nearly horizontal rows of scutes (assemblage of somewhat enlarged scales) on abdomen between pectoral and pel-

Table 3. Morphometrics as % of SL2 (anterior tip of maxillary to middle of caudal-fin base) of *Allocyttus folletti and A. verrucosus*.

Characters	*A. folletti*			*A. verrucosus*	
	Emperor Seamounts N=21	Japan N=2	Myers (1960)[1] N=3	Examined specimens N=7	Gilchrist (1906)
SL2 (mm)	264.7–526	187.4–286.1	341 (160–341)	107.4–232.8	?
HL2	32.8–37.1	33.8–38.0	35.8 (35.8–41.3)	38.8–40.8	*39.0*
PDFL2	49.1–57.2	51.3–53.7	*50.1*	51.2–60.9	*57.4*
PAFL2	55.5–64.5	56.7–69.1	*62.8*	68.5–80.5	*66.1*
BD1	51.2–56.6	53.4–56.1	*51.8*	59.5–69.4	*66.1*
BD2	52.3–58.7	53.9–56.6	54.3 (54.3–59.4)	59.2–66.4	*67.2*
DFBL	44.4–51.0	44.8–47.9	50.2 (47.2–50.2)	45.1–49.3	*50.2*
AFBL	39.4–43.7	39.2–43.9	40.8 (38.9–42.5)	37.7–41.7	*42.6*
HW	19.3–22.6	19.9–21.7	—	20.3–23.6	—
UJL	14.3–17.0	15.2	16.1 (15.9–18.1)	15.1–19.4	*18.9*
LJL	20.2–22.7	21.6	19.9 (19.9–23.8)	22.7–25.5	*24.2*
ED	12.7–18.7	16.4–18.4	*14.5* (—)	15.4–19.2	*19.0*
SNL	8.6–14.2	9.6	10.3 (10.3–12.5)	10.4–13.9	*13.5*
LW	1.7–2.5	1.8–2.1	*2.1*	2.5–3.7	*4.3*
P1L	14.5–17.8	15.3–15.4	16.7 (15.9–19.4)	16.5–20.6	*19.0*
P2L	14.5–19.5	17.1–19.7	—	19.4–24.6	*19.7*
DS2L	8.5–11.1	10.2–10.8	8.4 (8.4–11.9)	7.6–11.9	*8.2*
DRL	11.8–15.0	13.1–14.7	12.0 (11.1–13.8)	15.0–18.0	*18.8*
AS1L	5.3–7.7	6.9	—	6.1–7.1	*6.6*
ARL	14.0–15.7	14.1–16.8	13.5 (13.1–16.3)	15.9–18.7	*19.1*
P2SL	11.4–16.3	15.3–16.7	13.2 (13.2–22.5)	11.3–16.9	—
TEL	15.2–18.7	16.6–18.0	17.6 (17.6–19.1)	21.1–25.1	—
AEL	14.7–20.4	18.2–18.7	18.8 (18.8–20.2)	20.9–26.7	
P2O-AFO	18.0–23.4	20.6–21.3	—	23.7–30.3	—
CPL1	11.3–15.1	12.4–14.7	*13.5*	7.9–10.6	*12.3*
CPL2	10.5–13.2	11.2–13.9	—	6.3–9.3	—
CPD	5.0–6.8	5.7–6.3	5.9 (5.9–6.3)	6.1–7.0	*7.2*

Abbreviations: AEL, abdominal edge length; AFBL, anal-fin base length; ARL, longest anal-fin ray length; AS1L, 1st anal-fin spine length; BD1, body depth 1; BD2, body depth 2; CPD, caudal-peduncle depth; CPL1, caudal peduncle length 1; CPL2, caudal-peduncle length 2; DFBL, dorsal-fin base length; DRL, longest dorsal-fin ray length; DS2L, 2nd dorsal-fin spine length; ED, eye diameter; HL2, head length 2; HW, head width; LJL, lower-jaw length; LW, lachrymal width; P1L, pectoral-fin length; P2L, pelvic-fin length; P2SL, pelvic-fin spine length; PAFL2, pre-anal fin length 2; PDFL2, pre-dorsal fin length 2; P2O-AFO, length from pelvic-fin origin to anal-fin origin; SNL, snout length; TEL, thoracic edge length. For methods of measurements, refer to text. [1] Data of holotype, and range of holotype+two paratypes in parentheses. Digits in italics indicating measurements from figures of original description.

vic fins; in upper row enlarged scales forming 1–5 patches, weak or dislodged in some specimens; in lower row, enlarged scales forming continuous row (Fig. 3A). Body uniformly dark brown or grayish brown, fins darker; cheek and opercles blueish.

Distribution. Emperor Seamounts (Mundy 2005; present study), Bering Sea and Pacific Ocean east to Central California and west to Japan (from Hokkaido to Ibaraki Prefecture) (Mecklenburg et al. 2002; Nakabo and Kai 2013).

Discussion

Identification. Four genera are recognized in the family Oreosomatidae (James et al. 1988; Yearsley and Last 1998): *Pseudocyttus* Gilchrist, 1906, *Oreosoma* Cuvier, 1829, *Neocyttus* Gilchrist, 1906, and *Allocyttus* McCulloch, 1914. The present specimens are identified as *Allocyttus*, being distinguished from the other genera by the following combination of characters (see James et al. 1988): from *Pseudocyttus* by having the first dorsal-fin spine shorter than the second (vs. longer in *Pseudocyttus*), and six pelvic-fin soft rays (vs. five); from *Oreosoma* by having radiating striations and lacking a horizontal ridge on the opercle (vs. lacking radiating striations and having a prominent horizontal ridge), and relatively small eye diameter (39–46% vs. 52–60% of HL1); and from *Neocyttus* by having a nearly straight or slightly convex predorsal profile (vs. strongly concave and sharply risen).

Within the genus *Allocyttus*, the present specimens can be easily distinguished from *A. niger* (see James et al. 1988), in lacking spinules on the dorsal and anal-fin rays (vs. spinules present), fewer total gill rakers (20–27 vs. 26–33), and fewer lateral-line scales (82–93 vs. 91–102). From *A. guineensis* (see Trunov 1982; Heemstra 2016), the present specimens differ in having more anal-fin rays (29–32 vs. 26–27), a shorter head length (HL1: 34.6–39.3% vs. ca. 40–45% of SL1), a longer 2nd dorsal-fin spine (8.4–11.0% vs. 4.6–5.7% of SL1) and a longer 1st anal-fin spine (5.2–7.6% vs. 1.7–4.4% of SL1).

Comparisons of the present specimens with the holotype

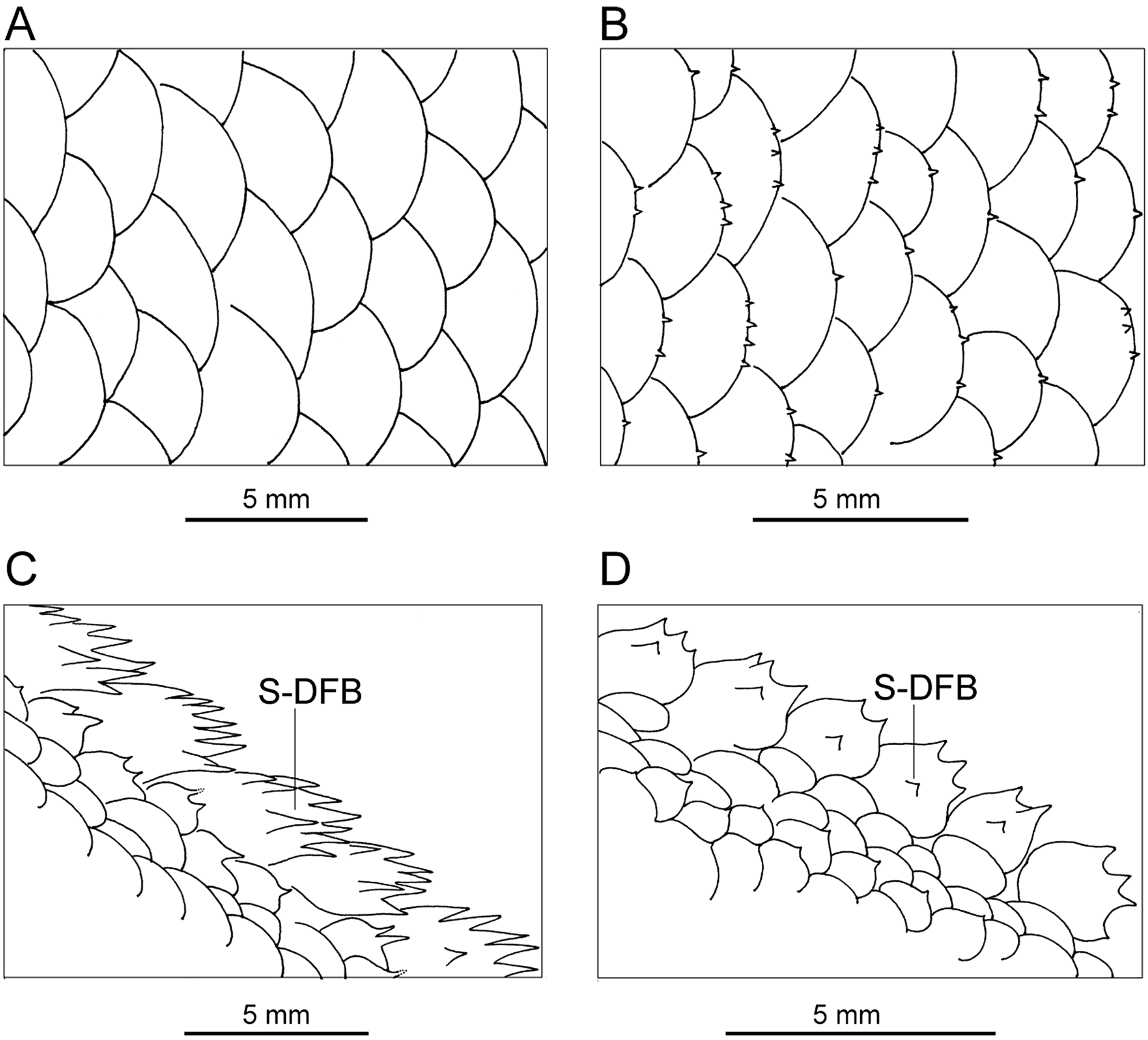

Fig. 2. Scales on mid-side of body in, (A) *Allocyttus folletti*, FAKU 72575, 397 mm SL, Emperor Seamounts, and (B) *Allocyttus verrucosus,* NSMT-P 113107, 238.4 mm SL, Australia; enlarged scales of dorsal-fin base (S-DFB) in (C) *A. folletti*, SNFR 22403, 289.3 mm SL, Emperor Seamounts, and (D) *A. verrucosus,* BSKU 48476, 136.5 mm SL, off South Africa.

of *A. folletti* and with *A. verrucosus* [comparative specimens, and one of the syntypes based on the illustration in Gilchrist (1906)] are presented in Tables 1–3. The ranges for most of the characters in the present specimens include the value for the holotype of *A. folletti.* However, there are many characters that disagree with the characters in *A. verrucosus,* including with respect to meristics (Table 1), more dorsal- and anal-fins spines+rays (37–40 vs. 34–37 and 32–35 vs. 29–32 respectively), more total vertebrae (37–40 vs. 35–37) and more S-DFB (31–42 vs. 26–31) and S-AFB (29–37 vs. 25–28). With respect to morphometrics (Tables 2, 3), the present specimens disagreed with *A. verrucosus* in having a smaller head (HL1: 34.6–39.3% vs. 40.2–43.1% of SL1; HL2: 32.8–38.0% vs. 38.8–40.8% of SL2), a shorter preanal-fin length (PAFL1: 53.8–62.4% vs. 64.5–82.0% of SL1; PAFL2: 55.5–69.1% vs. 68.5–80.5% of SL2), a shallower BD1 (50.4–55.9% vs. 56.9–68.7% of SL1; 51.2–56.6% vs. 59.5–69.4% of SL2), a narrower LW (1.7–2.5% vs. 2.5–4.2% of SL1; 1.7–2.5% vs. 2.5–4.3% of SL2), a longer CPL1 (11.2–14.8% vs. 7.7–11.9% of SL1; 11.3–15.1% vs. 7.9–12.3% of SL2) and CPL2 (10.4–13.8% vs. 6.1–8.9% of SL1; 10.5–13.9% vs. 6.3–9.6% of SL2), a shorter DRL (11.6–14.7% vs. 14.6–18.2% of SL1; 11.8–15.0% vs. 15.0–18.8% of SL2), a shorter TEL (14.6–18.5% vs. 20.6–24.9% of SL1; 15.2–18.7% vs. 21.1–25.1% of SL2), a shorter AEL (14.6–20.2% vs. 20.1–26.0% of SL1; 14.7–20.4% vs. 20.9–26.7% of SL2) and a shorter P2O-AFO (17.7–23.1% vs. 23.9–29.6% of SL1; 18.0–23.4% vs. 23.7–30.3% of SL2). In addition, the caudal peduncle was deeper posteriorly (Fig. 1C, D) and CFD was 140–188% of CPD in the examined specimens, agreeing with the holotype of *A. folletti* (180%) and greater than in *A. verrucosus* (111–127% in comparative specimens).

The scales of the entire mid-lateral area, lateral line, and caudal peduncle of the examined specimens are cycloid, agreeing with the holotype of *A. folletti* (see Myers 1960), and differing from the ctenoid scales in *A. verrucosus* (James et al. 1988; present study) (Fig. 2A, B). In *A. folletti*, the maximum number of spines of S-DFB and S-AFB is 7–12

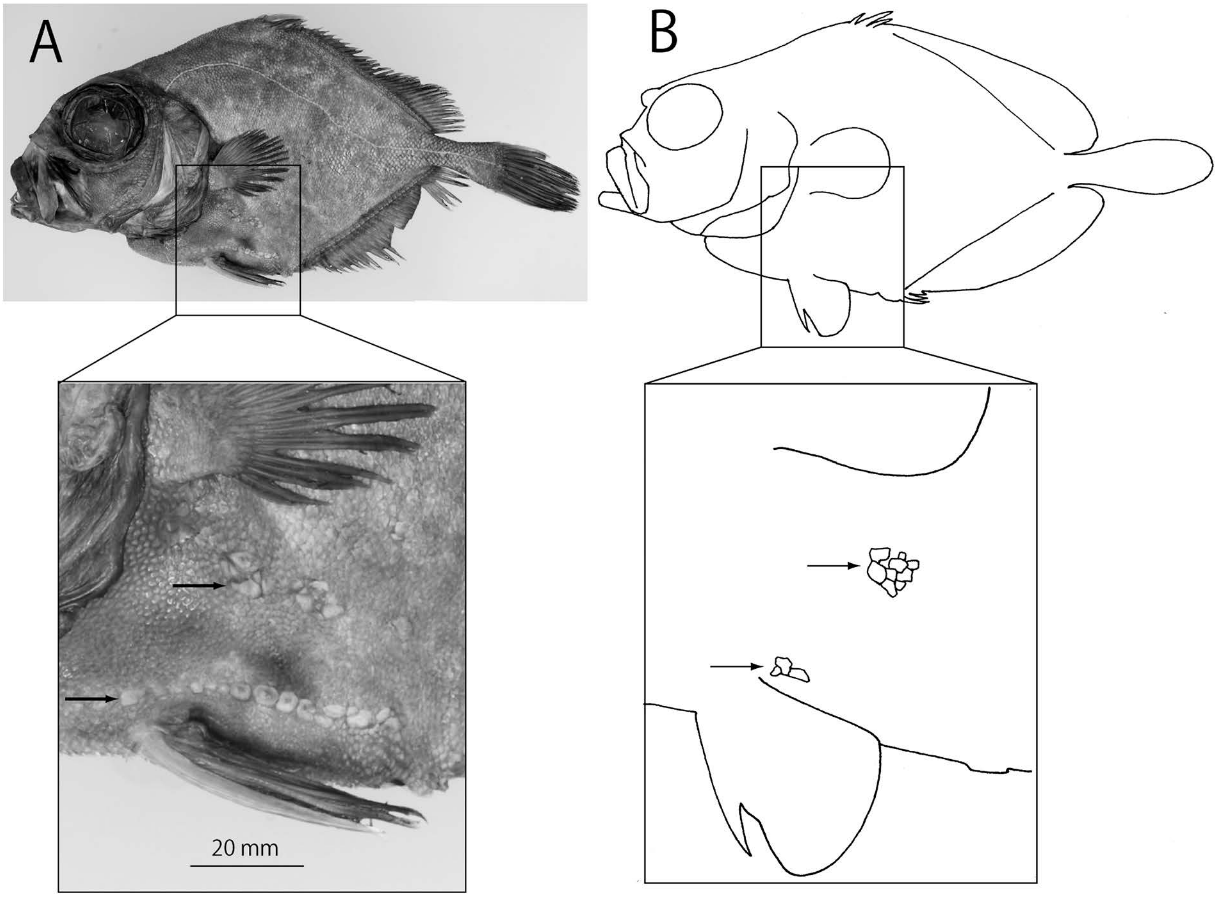

Fig. 3. Lateral aspect (above) and abdomen (below) of *Allocyttus folletti*. A, SNFR 10560, 293.4 mm SL, Emperor Seamounts; B, CAS-SU 15377, holotype of *Allocyttus folletti*, off California, traced from Myers (1960: fig. 1). Arrows indicate the rows of scutes.

(margin)+1–3 (center) (Fig. 2C), whereas in *A. verrucosus* it is 3–6 (margin)+1–2 (center) (Fig. 2D). James et al. (1988) described *A. verrucosus* as having a "row of ctenoid scales along bases of dorsal and anal fin with up to 6 spines per scale" and this agrees with our observations in *A. verrucosus*. These data demonstrate that the examined specimens from the Emperor Seamounts and Japan represent *A. folletti*, not *A. verrucosus*.

The two rows of abdominal scutes (serial enlarged scales), thought to be one of the diagnostic characters of *A. verrucosus* (Myers 1960; Abe and Hotta 1962; Kido 1983), were observed in the examined specimens (Fig. 3A), although their degree of development was variable. In addition, the original picture of the *A. folletti* holotype (Myers 1960: fig. 1) shows a small patch of somewhat enlarged scales on the mid-lateral abdomen between the pectoral and pelvic fins, and another patch above the pelvic fin (Fig. 3B). Based on their shape and position, these scale patches are akin to the scutes typical of *A. verrucosus*. Accordingly, the presence or absence of scutes is not a valid character to distinguish *A. verrucosus* from *A. folletti*. Mecklenburg et al. (2002) noted that *A. verrucosus* was different from *A. folletti* in having more cones (=scutes; 7 or more vs. 3–5 in *A. folletti*: Mecklenburg et al. 2002; Kamiyama 2017) in the upper abdominal row. In the examined specimens, the number of scutes in *A. folletti* was 1–5, and in *A. verrucosus* was 6–10 in six specimens but in one specimen (BSKU 48478), no scute was observed on either side. The variation and significance of this character needs verification.

The abdominal scutes of prejuvenile *A. folletti* are each a remarkably enlarged, cone-like solitary scale (e.g., Kobayashi et al. 1968; Hart 1973; Nakabo 2002), while in the examined adult specimens the scutes are an assemblage of hypertrophied scales (Fig. 3). This indicates that the state of each *A. folletti* scute changes ontogenetically. Mecklenburg et al. (2002) noted that the rows of scutes were reduced or lost in adults, but all the specimens examined here retained their scutes (although some were dislodged) even in the largest specimen (537 mm SL). The degree of scute reduction in adults appears to be variable between individuals.

The characters of specimens reported as *A. verrucosus* from Japan and adjacent waters are presented in Table 4. They agree well with *A. folletti* but not with *A. verrucosus* (see also Tables 1, 2). Recently, Amaoka et al. (2020) published pictures of an adult and a juvenile oreosomatid (supposedly from Hokkaido, Japan) identified as *A. folletti*. In the adult specimen, the mouth is strongly projected, negating the value of any measurements from the snout tip (e.g., SL1) and thus it is not listed in Table 4. However, from the measurement of the picture of the adult specimen, the percentage in SL2 of BD1 (53.0%), BD2 (53.5%) and CPL2 (11.0%) agree with *A. folletti* but not *A. verrucosus* (see

Table 4. Characters of oreosomatid reported from the western North Pacific as *Allocyttus verrucossus* but reidentified as *A. folletti* in this study.

		Meristics					Morphometrics (% of SL1)								
	N	DFS+DFR	AFS+AFR	TV	S-DFB	S-AFB	HL1	BD1	PAFL1	CPL1	CPL2	TEL	AEL	SMS	Locality
Abe & Hotta (1962)	1	40	34	—	—	—	39.2	50.8	56.4	*12.2*	—	16.0	—	—	off NE of Japan
Kobayashi et al. (1968)[1]	3	39–42	33–34	39	32–33[2]	29[2]	37.8	51.7	58.1	*12.0*	—	17.5	18.0	Cy	Bering Sea/N Pacific
Maruyama (1970)	1	39	33	—	35	30	40.4	50.3	*61.3*	*11.9*	—	—	—	Cy	off NE of Japan
Kido (1983)	1	40	35	41	—	—	35.7	52.5	—	*12.1*	—	—	—	Cy	off NE of Japan
Ida et al. (1992)	1	—	—	—	—	—	37.5	53.2	*59.8*	—	—	—	—	—	off NE of Japan
Amaoka et al. (1995)	1	—	—	—	—	—	*36.1*	*51.3*	*62.0*	*11.7*	—	—	—	—	off NE of Japan
Kitagawa et al. (2008)	1	—	—	—	—	—	32.9	52.7	55.6	*14.8*	*12.1*	—	—	—	off NE of Japan
Integrated range		39–42	33–35	39–41	32–35	29–30	32.9–40.4	50.3–53.2	*55.6–62.0*	*11.7–14.8*	*12.1*	16.0–17.5	18.0		

Abbreviations: AEL, abdominal edge length; AFR, anal-fin rays; AFS, anal-fin spines; BD1, body depth 1; CPL1, caudal-peduncle length 1; CPL2, caudal-peduncle length 2; Cy, cycloid; DFR, dorsal-fin rays; DFS, dorsal-fin spines; HL1, head length 1; PAFL1, preanal-fin length 1; S-AFB, enlarged scales of anal-fin base; S-DFB, enlarged scales of dorsal-fin base; SMS, scale on middle side of body; TEL, thoracis edge length; TV, total vertebrae. For methods of measurements, refer to text. Digits in italics indicate measurements from pictures in references. [1] Morphometrics of juveniles excluded. [2] Reported as 29 for S-DFR and 32–33 for S-AFB but considered incorrect (discussed in text).

Table 3). HL2 is 39.2% of SL2 (beyond the range of *A. folletti*) but this variation is probably due to damage of the opercular elements, viz., it appears the subopercle and interopercle are lost and the opercle is rotated backward from its original position. We therefore consider these individuals to represent *A. folletti*, not *A. verrucosus*.

We conclude that the oreosomatid of the western North Pacific Ocean is *A. folletti*, supporting the arguments of James et al. (1988), Mecklenburg et al. (2002) and Nakabo and Kai (2013).

Distinction of *A. folletti* from *A. verrucosus*. Characters seemingly useful for distinguishing *A. folletti* and *A. verrucosus* in Tables 1–3 are compared with literature data (Table 5) to test their validity. In the meristic characters, dorsal-fin spines+rays (36–42 vs. 33–38), anal-fin spines+rays (31–35 vs. 27–33), and total vertebrae (37–41 vs. 34–38) are useful, although the ranges of the two species overlap. S-DFB (31–42 vs. 26–31) and S-AFB (29–37 vs. 25–28) are likely to be useful, although the available data from references are limited. Kobayashi et al. (1968) reported that based on three specimens the number of "rough scales along to dorsal base" (=S-DFB) was 29, and the number of "rough scales along to anal base" (=S-AFB) as 32–33. However, the correct counts of S-DFB and S-AFB are likely to be 32–33 and 29 respectively, because the number of S-DFB is greater than the number of S-AFB in most (21 of 23) of the specimens examined here; it is not likely that S-DFB was fewer than S-AFB in all of the three specimens of Kobayashi et al. (1968). Unfortunately, the picture of the specimen in Kobayashi et al. (1968: pl. 1a) is not clear enough to count the number of S-DFB and S-AFB correctly, although the rough counts based on an enlarged copy (200%) of the picture were ca. 33 and ca. 30 respectively. Ward et al. (1996) raised the number of pectoral-fin rays as a character to distinguish *A. folletti* and *A. verrucosus* (19–21 vs. 17–19 respectively). However, the data of the present study (Table 1) and those of the references in Table 5 revealed the wider overlapping range (19–21 vs. 17–21 respectively).

In the morphometric characters as % of SL1 (Table 5; data of juveniles are neglected), shorter PAFL1 (53.8–63.6% vs. 64.8–83.7%) and longer CPL2 (10.4–15.6% vs. 6.1–10.2%) seem especially useful because the two species were clearly separated by these characters. HL1 (32.9–40.4% vs. 38.5–48.4%), TEL (14.6–18.5% vs. 17.8–28.0%), AEL (14.6–20.2% vs. 20.1–26.0%) and CPL1 (11.2–14.8% vs. 7.7–11.8%) seem useful although the ranges of the two species overlap. The range of BD1 in *A. verrucosus* (46.0–77.9%) includes the whole range in *A. folletti* (50.3–55.9%). However, the data of *A. verrucosus* in James et al. (1988) from the specimens of South Africa (46.0–73.3%) and Australia (53.5–77.9%) include exceptionally low values (46.0% and 53.3%), which might be mistakes or abnormalities. If these values are excluded, available data of this character in *A. verrucosus* is 56.5–77.9%, clearly separable from *A. folletti* (50.3–55.9%). The significance of the last character needs further verification.

The caudal peduncle in *Allocyttus folletti* is deeper posteriorly compared to that of *A. verrucosus* (Fig. 1C, D); when the depth of caudal-fin base (CFD) is expressed as a per-

Table 5. Meristics and morphometrics thought to be useful to distiguish *Allocyttus folletti* and *A. verrucosus*.

			Meristics					Morphometrics (% of SL1: snout tip–middle of caudal-fin base)							Locality
Species	Sources	N	DFS+DFR	AFS+AFR	TV	S-DFB	S-AFB	HL1	BD1	PAFL1	CPL1	CPL2	TEL	AEL	
A. folletti	Present study	23	37–40	32–35	37–40	31–42	29–37	34.6–39.6	50.4–55.9	53.8–62.4	11.2–14.8	10.4–13.8	14.6–18.2	14.6–20.2	Emperor Seamouts & Japan
	seven references[1,2]	9	39–42	33–35	39–41	32–35	29–30	*32.9*–40.4	50.3–*53.2*	55.6–*62.0*	*11.7–14.8*	*12.1*	16.0–17.5	18.0	Western N Pacific
	Welander (1957)	1	40	35	—	—	—	—	—	—	—	—	—	—	N Pacific
	Myers (1960)[2]	3	37–39	34–35	—	—	—	36.3–38.2	—	62.9–63.6	*12.6*	—	17.3–18.5	18.4–19.7	off California
	Miller and Lea (1972)	?	36–40	—	—	—	—	—	—	—	—	—	—	—	off California
	Hart (1973)[2]	1	40	35	—	—	—	—	—	—	—	—	—	—	off British Colombia
	Anderson et al. (1979)	2	39	34	39	—	—	—	—	—	—	—	—	—	off California
	Gillespie and Saunders (1994)	1	40	34	—	—	—	—	—	—	—	—	—	—	off British Colombia
	Ward et al. (1996)	8	38–39	31–34	39	—	—	—	—	—	—	—	—	—	?
	Mecklenburg et al. (2002)	?	—	33–35	39–41	*31*	*33*	*35.0*	*54.8*	*58.4*	*14.6*	*15.6*	—	—	off Alaska
	Kamikawa (2017)	1	—	—	—	—	—	*39.6*	*53.6*	*62.3*	*11.7*	*10.4*	—	—	U. S. West Coast
	Integrated range		36–42	31–35	37–41	31–42	29–37	*32.9–40.4*	50.3–55.9	53.8–63.6	11.2–14.8	10.4–*15.6*	14.6–18.5	14.6–20.2	
A. verrucosus	Present study	7	34–36	29–31	35–37	26–31	25–28	40.2–43.1	56.9–68.7	66.5–82.0	7.7–10.2	6.1–8.9	20.6–24.9	20.1–26.0	New Zealand/South Africa
	Gilchrist (1906)	1	37	32	—	—	—	*41.1*	*63.0*	*64.8*	*11.8*	—	—	—	South Africa
	McCulloch (1914)	8	36–38	—	—	—	—	—	—	—	—	—	—	—	S Australia
	Trunov (1982)	5	—	—	—	—	—	—	57.5–63.0	65.3–71.5	—	—			E Atlantic
	Shimizu (1983)	2	—	29–30	—	—	—	*40.6*	*65.4*	*76.5*	*8.9*	—	—	—	off Suriname/Guiana
	Karrer (1986b)	?	—	—	—	—	—	ca. 37–45	ca. 59–71	—	—	—	—	—	South Africa
	James et al. (1988)	144	33–37	27–33	34–37	—	—								Following three areas
	(New Zealand)	(51)						39.4–45.8	56.5–75.7	68.7–83.7	—	—	20.6–28.0	—	New Zealand
	(Australia)	(44)						38.5–48.4	53.5–77.9	66.0–82.2	—	—	17.9–28.0	—	Australia
	(South Africa)	(49)						39.8–46.7	46.0–73.3	65.3–79.0	—	—	17.8–26.5	—	South Africa
	James and Inada (1990)	59	34–37	28–32	—	—	—	*41.3*	*61.1*	*72.9*	*8.6*	*8.5*	—	—	New Zealand
	DuBuit and Quéro (1993)	1	37	31	—	—	—	—	—	—	—	—	—	—	N Atlantic
	Ward et al. (1996)	9	35–37	29–31	36–38	—	—	—	—	—	—	—	—	—	Australia
	Bray (2008)	?	—	—	—	—	—	ca. 38–49	*55.4*	*68.9*	*9.9*	—	—	—	S Australia
	Morris et al. (2011)	1	—	32	—	—	—	—	—	—	—	—	—	—	Labrador Sea, Canada
	Kloppmann and Thiel (2013)[2]	16	35–38	29–33	36–38	—	—	40.0	—	67.3	—	10.2	20.4	20.4	Greenland/SW Indian Ocean
	Bray (2015)	?	—	—	34–37	—	—	*38.9*	*56.6*	*70.2*	*8.5*	—	—	—	New Zealand
	Heemstra (2016)	?	—	—	34–37			ca. 37–45	ca. 59–71	—	—	—	—	—	Eastern Central Atlantic
	Integrated range		33–38	27–33	34–38	26–31	25–28	38.5–48.4	46.0–77.9	*64.8*–83.7	7.7–*11.8*	6.1–10.2	17.8–28.0	20.1–26.0	

Abbreviations: AEL, abdominal edge length; AFR, anal-fin rays; AFS, anal-fin spines; BD1, body depth 1; CPL1, caudal-peduncle length 1; CPL2, caudal peduncle length 2; DFR, dorsal-fin rays; DFS, dorsal-fin spines; HL1, head length 1; PAFL1, preanal-fin length 1; S-AFB, enlarged scales of anal-fin base; S-DFB, enlarged scales of dorsal-fin base; SL1, standard length 1; TEL, thoracis edge length; TV, total vertebrae. For methods of measurements, refer to text. Digits in italics indicate measurements from pictures in references. [1] Integrated data from Abe and Hotta (1962), Kobayashi et al. (1968), Maruyama (1970), Kido (1983), Ida et al. (1992), Amaoka et al. (1995) and Kitagawa et al. (2008) (see Table 4). [2] Morphometrics of juveniles excluded.

centage of caudal-peduncle depth (140–188% vs. 111–127% in the examined specimens) it seems a useful character. This can be seen in the figures in the references (cited in Tables 4, 5) although accurate measurement based on these figures is difficult in many cases.

Ward et al. (1996) pointed out that *A. folletti* has a narrower lachrymal width (LW) than in *A. verrucosus* (1.7–2.4% vs. 3.3–4.0% of SL respectively). In our observation, this character clearly separated the two species (Tables 2, 3), supporting the validity of this character. But note that SL of Ward et al. (1996) was measured from between lachrymal tips anteriorly, and thus cannot be directly compared with our study. Ward et al. (1996) pointed out that *A. folletti* has longer fin spines (e.g., 2nd dorsal-fin spine: 7.6–12.6% vs. 5.4–9.1% of SL), but from the wide range of overlapping, it is often difficult to identify the specimens by this character alone (see also Tables 2, 3).

Scales of mid-side (SMS) are cycloid in *A. folletti* and ctenoid in *A. verrucosus* (Fig. 2A, B) making this a useful character to separate the two species. Furthermore, the numbers of spines on the margin of S-DFB and S-AFB (up to 7–12 vs. up to 3–6) differ between the two species based on the examined specimens. The data in the holotype of *A. folletti* (up to nine) and *A. verrucosus* in James et al. (1988) (up to six) agree with our observations.

The adherence of the scales was thought to be a character to separate the two species. Abe and Hotta (1962) identified their specimen of oreosomatid from Japan as *A. verrucosus* and not *A. folletti* partly because of the "tenacious" (= adherent) scales, in addition to the scutes. Direct comparisons of the two species revealed that the mid-side scales are, overall, preserved better in *A. verrucosus*, and those scales were more easily removed by tweezers in *A. folletti.* However, Abe and Hotta (1962) apparently judged the scale condition as "tenacious" without comparison with the "real" *A. verrucosus*. In the specimen of Abe and Hotta (1962: figs 1, 3) the scales look well preserved; this may have led to these authors describing the scales as "tenacious" and misidentifying the specimen as *A. verrucosus*.

Myers (1960: 93) listed the following "subtle features" to distinguish *A. folletti* from *A. verrucosus*: (1) more concave predorsal profile, (2) flatter belly, (3) snout less smoothly rounded down, and (4) more prominent and rugose nasal boss (=bony projection). Regarding the predorsal profile (1), however, in *A. folletti* it was usually (in 18 of 23 specimens examined) slightly convex between the dorsal-fin origin and the vertical through the posterior end of the gill opening (Figs 1A, 3). In *A. verrucosus*, the corresponding part was slightly concave (Fig. 1B) in six of seven comparative specimens. The same conditions can be observed in various photos and illustrations of *A. folletti* [e.g., Myers 1960 (holotype: Fig. 3); Abe and Hotta 1962; Kobayashi et al. 1968; Machida 1984; Mecklenburg et al. 2002; Amaoka et al. 2020), and those of *A. verrucosus* (e.g., Gilchrist 1906; McCulloch 1914; Shimizu 1983; James et al. 1988; James and Inada 1990; Bray 2008, 2015; Kloppmann and Thiel 2013). However, the relevant part of the predorsal contour was straight in some specimens of both species, and thus this character is not always useful to distinguish the two species. Regarding the shapes of the belly (2) and snout (3), we did not recognize any significant differences between the two species. The nasal boss (4) was more strongly projected (Fig. 1E, F) and armed with larger spinules in *A. folletti* (except the smallest specimen examined: NSMT-P 30689, 190.7 mm SL), as described by Myers (1960).

Note on distribution. In the Emperor Seamounts, *Allocyttus folletti* was previously reported from Koko Seamount (35°30′N, 171°30′E) and northward to Suiko Seamount (44°34′N, 170°24′E) (see Mundy 2005). The present study extends the range southward from Koko Seamount to Hancock Seamounts. The latter comprises two seamounts, Southeast Hancock (29°48′N, 178°05′E) and Northwest Hancock (30°17′N, 178°44′E) (Boehlert 1988). The specimen we examined (FAKU 119906) was collected from Hancock Seamounts but its exact locality is unknown.

Biological features and management suggestions. The largest specimen examined in the present study was 537 mm SL (630 mm in total length=TL) considerably larger than the largest specimen of *A. verrucosus* in the review of James et al. (1988), 265 mm SL (320 mm TL). The maximum size of *A. verrucosus* reported by Lyle and Smith (1997) in an abundance and biological survey of oreos in south-eastern Australia was ca. 390 mm TL (the corresponding SL is unknown but estimated as ca. 325 mm). These data suggest that *A. folletti* reaches a larger maximum size than *A. verrucosus*.

Stewart et al. (1995) estimated that for *A. verrucosus* from western Bass Strait, Australia, the age at maturity was 28 years in females and 24 years in males, and the maximum age was 130–170 years for fish of 34–35 cm TL. From the estimated low fecundity, high age at maturity and longevity, Stewart et al. (1995) noted the susceptibility of *A. verrucosus* to over-exploitation. Although the age, growth, and maturity of *A. folletti* are not understood, similar biological features are anticipated due to its close affinity with, and similar deep-sea habitat to, *A. verrucosus*. Collecting biological information of this species, including its life history and genetics, under the valid scientific name *A. folletti*, is required to understand its subpopulations and vulnerability, and to sustainably manage its exploitation.

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