

Rediagnosis of *Onigocia grandisquama* (Actinopterygii: Perciformes: Platycephalidae) and Comparison with Congeners

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A platycephalid fish, *Onigocia grandisquama* (Regan, 1908) is rediagnosed based on 52 specimens, including the holotype, from the Indo-West Pacific. Geographic variation in the species was recognized in the number of pectoral-fin rays, the first example of such variation in fin ray counts in the Platycephalidae. The species displays wide intraspecific variation in the numbers of lachrymal, preocular, suborbital, and pterotic spines, with values for the first two overlapping with those of the very similar *Onigocia spinosa* (Temminck and Schlegel, 1843), making it difficult to separate the two. *Onigocia grandisquama* can be distinguished from *O. spinosa*, as well as from *Onigocia macrocephala* (Weber, 1913) and *Onigocia macrolepis* (Bleeker, 1854), which share with *O. grandisquama* an ocular flap on the posterior part of the eye, in lacking spines on the inner, middle, and/or outer ridges of the lachrymal. The generally greater number of pterotic spines also helps to separate *O. grandisquama* from its three congeners.

Key Words: geographic variation, intraspecific variation, *Onigocia spinosa*.

Introduction

Onigocia grandisquama was originally described by Regan (1908) from a single specimen collected in the Amirante Islands (as Amirantes), Seychelles, in the western Indian Ocean (Fig. 1A, B). Although Imamura and Sakashita (1997) and Imamura and McGrouther (2008) redescribed the species, their studied materials were collected from limited areas (the holotype and an additional specimen from the Gulf of Thailand for the former, and 13 specimens from Queensland, eastern Australia for the latter) and its intraspecific variation remained poorly known. In the present study 52 specimens of *O. grandisquama* from the Indo-West Pacific were examined, including the holotype (Fig. 2). Wide intraspecific variation in four meristic characters was found, reducing the utility of two of them for separating this species from the very similar *Onigocia spinosa* (Temminck and Schlegel, 1843). The presence or absence of spines on the inner, middle, and outer ridges of the lachrymal proved to be useful for this purpose, however. In this paper I provide a detailed account of the morphological variation in the species, with special attention to taxonomic characters suitable for separating *O. grandisquama* from *O. spinosa* and other congeners.

Materials and Methods

Counts and measurements were made according to Imamura (2008). Measurements were made with calipers to the nearest 0.1 mm. Terminology of head spines follows Knapp *et al.* (2000). The inner, middle, and outer ridges of the lachrymal are three ridges on the anterior portion of that bone, as defined by Imamura (2011). Institutional acronyms are from Sabaj Pérez (2014), except for the National Institute of Coastal Aquaculture, Thailand (NICA). Standard and head lengths are abbreviated as SL and HL, respectively.

Material examined. The following 52 specimens of *O. grandisquama* were studied. In the list they are provisionally divided into five regions for a comparison of geographic variation among them (Fig. 2).

Western Indian Ocean (12 specimens): BMNH 1908.3.23.209, holotype, 54.4 mm SL, Amirante Islands, Seychelles; USNM 303744, 7 specimens, 52.6–68.7 mm SL, north of Mauritius (11°05.00'S, 62°02.00'E), 58–61 m depth, 8 January 1989; USNM 346059, 4 specimens, 53.4–71.9 mm SL, off Somali coast, Somalia (10°00'N, 51°15'E), 59–61 m depth, 16 December 1964.

Eastern Indian Ocean (7 specimens): NTM S. 11335-009, 62.7 mm SL, Pandjang Island, southwestern Sumbawa, Indonesia (08°29'S, 116°58'E), 22–30 m depth, 15 August 1982; NTM S. 14363-012, 75.7 mm SL, northwest of Bassett Smith

Shoal, Timor Sea ($13^{\circ}13'7''\text{S}$, $125^{\circ}14'52''\text{E}$), 63 m depth, 12 June 1996; WAM P. 28754.009, 58.1 mm SL, North West Shelf, Australia ($19^{\circ}57'\text{S}$, $117^{\circ}54'\text{E}$), 22 April 1983; ZMA 112437, 4 paralectotypes of *Onigocia macrocephala* (Weber, 1913), 38.3–40.7 mm SL, Sapeh Strait, Indonesia, 69 m depth.

Coral Sea (31 specimens): BPBM 33845, 66.7 mm SL, Chesterfield Islands ($20^{\circ}40'9''\text{S}$, $158^{\circ}45'9''\text{E}$), 76 m depth, 22 August 1988; CSIRO H 6697-03, 2 specimens, 69.8–78.3 mm SL, east of Lizard Island, Queensland ($14^{\circ}41'\text{S}$, $145^{\circ}35'34''\text{E}$), 32 m depth, 19 November 2003; CSIRO H 6719-01, 2 specimens, 69.7–79.2 mm SL, east of Lizard Island, Queensland ($14^{\circ}40'\text{S}$, $145^{\circ}32'\text{E}$), 28 m depth, 19 November 2003; CSIRO H 6722-01, 52.1 mm SL, north-east of Cape York Peninsula, Torres Strait, Queensland ($10^{\circ}31'\text{S}$, $143^{\circ}51'\text{E}$ – $10^{\circ}32'\text{S}$, $143^{\circ}51'\text{E}$), 27 m depth, 10

January 2004; CSIRO H 6723-01, H 6723-04, 2 specimens, 75.7–91.4 mm SL, east of Bowling Green Bay, Queensland ($19^{\circ}15'\text{S}$, $147^{\circ}36'\text{E}$), 30 m depth, 1 December 2003; QM I. 23081, 71.8 mm SL, off Swan Reef, Queensland ($21^{\circ}13'\text{S}$, $150^{\circ}43'\text{E}$), 47 m depth, 16 September 1986; QM I. 36018, 68.2 mm SL, north of Cape Bowling Green, Queensland ($19^{\circ}05.1'\text{S}$, $147^{\circ}26.1'\text{E}$), 33 m depth, 23 November 2003; QM I. 36851, 37.1 mm SL, Blackwood Channel, Queensland ($11^{\circ}49.5'\text{S}$, $143^{\circ}40.5'\text{E}$), 4 February 2005; QM I. 37297, 3 specimens, 33.8–57.3 mm SL, north of Wainig Reef, Queensland ($14^{\circ}26.1'\text{S}$, $145^{\circ}14.1'\text{E}$), 9 February 2005; QM I. 37312, 70.9 mm SL, east of Chapman Island, Queensland ($12^{\circ}53.7'\text{S}$, $143^{\circ}45.3'\text{E}$), 26 January 2005; QM I. 37414, 71.2 mm SL, Black Rock Entrance, Queensland ($12^{\circ}14.7'\text{S}$, $143^{\circ}48.9'\text{E}$), 7 February 2005; QM I. 37419, 69.5 mm SL, northeast of Hadge Reef, Queensland ($13^{\circ}43.5'\text{S}$,

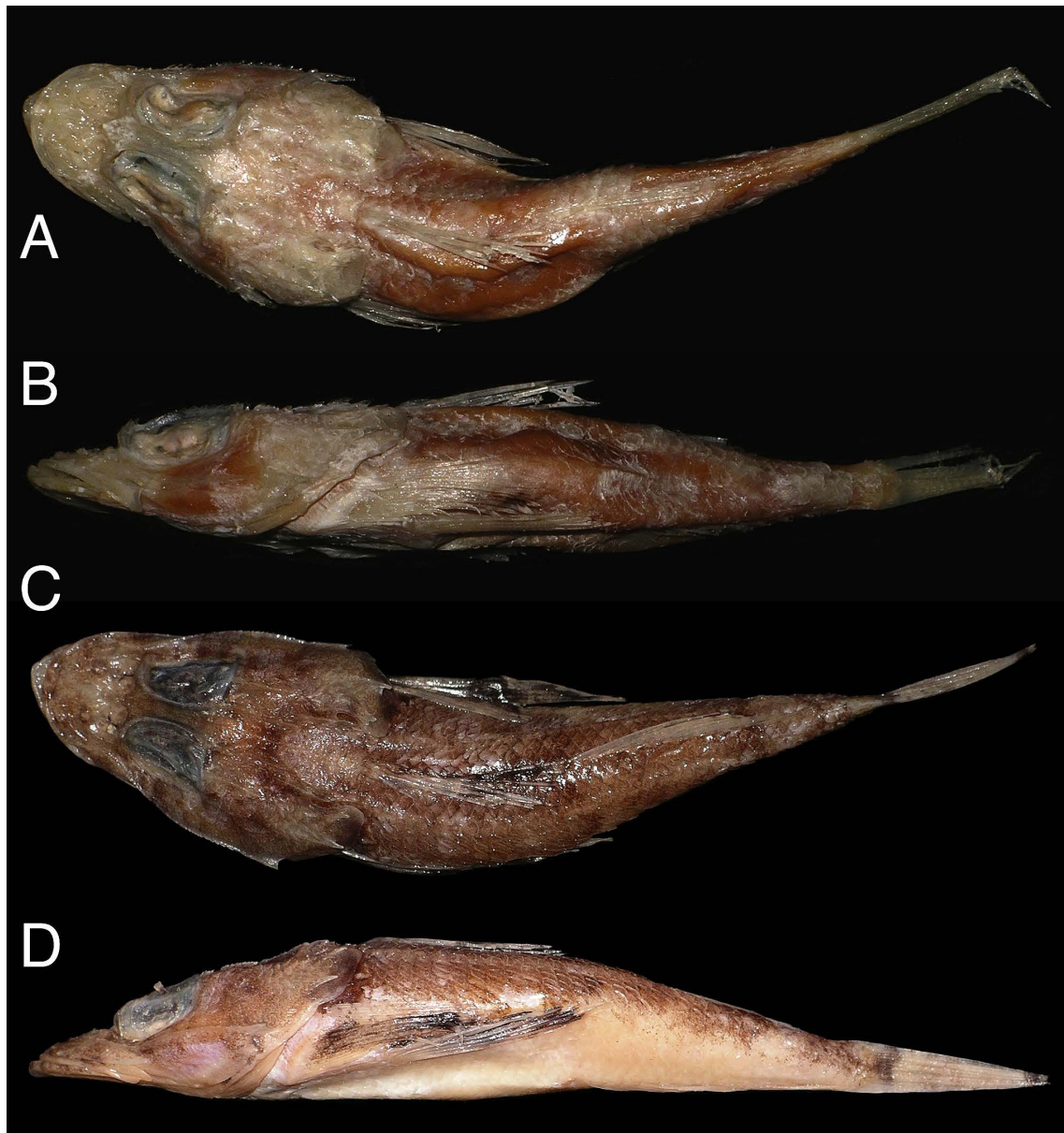


Fig. 1. *Onigocia grandisquama*. A–B, BMNH 1860.3.19.270, collected from the Amirante Islands, Seychelles, western Indian Ocean; C–D, QM I. 37419, 69.5 mm SL, collected from northeast of Hadge Reef, Queensland. A and C, dorsal views; B and D, lateral views.

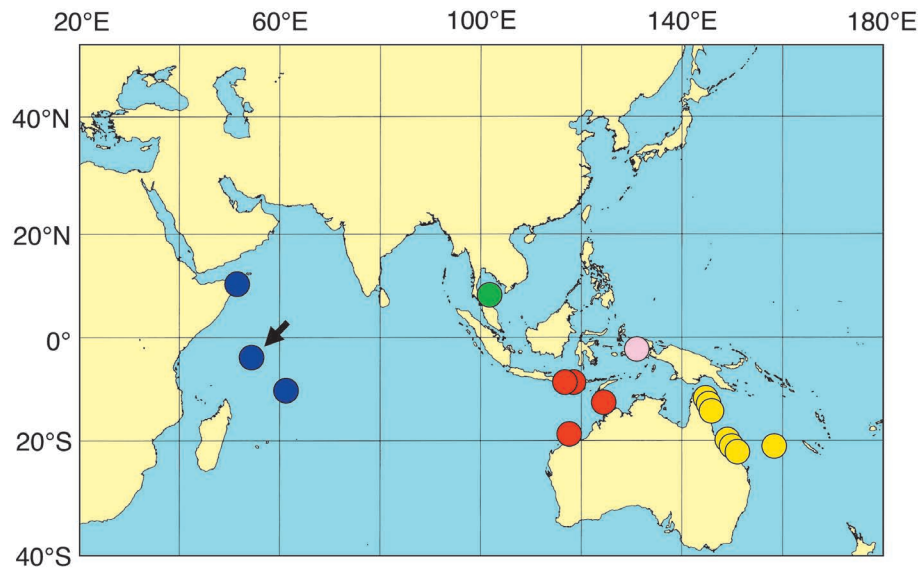


Fig. 2. Map showing collection localities of 52 examined specimens of *Onigocia grandisquama*. Blue, western Indian Ocean; red, eastern Indian Ocean; yellow, Coral Sea; pink, Ceram Sea; green, Gulf of Thailand. The arrow indicates the holotype.

144°7.5'E), 35 m depth, 18 January 2005; other one AMS and 12 QM specimens from Queensland were listed in Imamura and McGrouther (2008).

Ceram Sea (1 specimen): ZMA 124954, paralectotype of *Onigocia sibogae* Imamura, 2011, 40.2 mm SL, northwest of New Guinea (1°42.5'S, 130°47.5'E), 32 m depth.

Gulf of Thailand (1 specimen): NICA 242, 61.7 mm SL, Songkhla, 1982.

Comparative material. Other specimens of *Onigocia*, including type specimens of each species except for *O. macrolepis* which lacks extant types, are in the collections of AMS, BMNH, BPBM, CMNH, CSIRO, HUMZ, MNHN, NICA, NSMT, NTM, QM, RMNH, USNM, WAM and ZMA, as listed in Imamura and Knapp (2009) and Imamura (2011, 2012).

***Onigocia grandisquama* (Regan, 1908)**
(Figs 1, 4; Tables 1–3)

Platycephalus grandisquamis Regan, 1908: 239 (original description; type locality: Amirante Islands, Seychelles, western Indian Ocean).

Platycephalus macrocephalus Weber, 1913: 508, fig. 107 (original description; type locality: Sapeh Strait, Indonesia) (in part); de Beaufort and Briggs 1962: 146, fig. 36 (description; Sapeh Strait, Indonesia) (in part).

Platycephalus grandisquamis Weber, 1913: 509, fig. 108 [original description; type locality: northwest of New Guinea (1°42.5'S, 130°47.5'E)] (in part).

Onigocia grandisquamis: Matsubara and Ochiai 1955: 71 (discussion of generic assignment).

Onigocia grandisquama: Imamura 1996: 214 (discussion of generic assignment); Imamura and Sakashita 1997: 119, figs 1–4 (redescription; Amirante Islands, Seychelles, western Indian Ocean and Gulf of Thailand, western Pacific Ocean); Knapp *et al.* 2000: 8 (list of comparative

material; Amirante Islands, Mauritius, and Somalia, western Indian Ocean); Manilo and Bogorodsky 2003: S103 (list, Arabian Sea); Imamura and McGrouther 2008: 239, figs 1–2 (redescription, Queensland, eastern Australia); Imamura 2011: 59 (list of comparative material; Ceram Sea, Mauritius, and Somalia); Imamura 2012: 30 (list of comparative material; Sapeh Strait, Indonesia).

Diagnosis. A species of the genus *Onigocia* Jordan and Thompson, 1913 with the following characters: first dorsal-fin rays I+VII–VIII (usually I+VIII); second dorsal-fin rays 10–11 (usually 11); anal-fin rays 11–12 (usually 11); pectoral-fin rays 19–22; branched caudal-fin rays 9–10; pored lateral-line scales 32–39, anterior 2–8 scales each with a spine; gill rakers 1+4–5=5–6; lachrymal spines 2–5 (usually 2), tending to increase in number with growth; inner, middle, and outer ridges on lachrymal lacking spines; preocular spines 1–6, tending to increase in number with growth; sub-orbital spines 14–30, tending to increase in number with growth; pterotic spines 2–11, tending to increase in number with growth; HL 41.6–45.6% SL, single ocular flap present on posterior part of eye, not extending to its posterior margin; small, short papillae absent on posteromedial part of eye; upper iris lappet short and branched; notch absent on suborbital ridge below eye; interopercular flap absent; pelvic fin brownish to blackish, lacking distinct spots.

Distribution. *Onigocia grandisquama* has been recorded widely in the Indo-West Pacific, including the Amirante Islands, Seychelles (type locality; Regan 1908), Mauritius and Somalia (Knapp *et al.* 2000; this study), the Arabian Sea (Manilo and Bogorodsky 2003), Pandjang Island, Indonesia (new record), Sapeh Strait (Imamura 2012), North West Shelf, Australia (new record), Timor Sea (new record), Coral Sea, eastern Australia (Imamura and McGrouther 2008; this study), Chesterfield Islands (new record), Ceram Sea (Imamura 2011), and Gulf of Thailand (Imamura and Sakashita 1997) (see also Fig. 2).

Remarks. Table 1 shows counts and proportional measurements of this species from five geographical areas. See Imamura and Sakashita (1997) and Imamura and McGrouther (2008) for descriptions of characters (including coloration) not mentioned in the Diagnosis above.

A difference in the number of pectoral-fin rays was recognized between specimens from the Indian and western Pacific oceans in this study (Table 2). In addition, wider variations in the numbers of lachrymal, preocular, suborbital, and pterotic spines were found among these 52 specimens

than had previously been known (Fig. 3). However, the difference between pectoral-fin ray numbers in the two oceans was rather minor and the ranges mostly overlapped, and the greater variation in spine numbers appeared to be size-related, with larger specimens tending to have more spines. I conclude that the difference in numbers of pectoral-fin rays represents geographic variation, and the wide intraspecific variation in spine numbers represents change with growth in *O. grandisquama*. A detailed account of these characters is given below.

Table 1. Comparison of counts and proportional measurements of *Onigocia grandisquama* from five regions.

	Western Indian Ocean		Eastern Indian Ocean	Coral Sea	Ceram Sea	Gulf of Thailand
	Holotype	Others (<i>n</i> =11)	(<i>n</i> =7)	(<i>n</i> =31)	(<i>n</i> =1)	(<i>n</i> =1)
SL (mm)	54.4	51.1–71.9	38.3–75.7	33.8–91.4	40.2	61.7
Counts:						
First dorsal-fin rays	I+VIII	I+VIII (11)	I+VIII (7)	I+VII (2) or VIII (28)	I+VIII	I+VIII
Second dorsal-fin rays	11	11 (11)	10 (1) or 11 (6)	10 (1) or 11 (29)	11	11
Anal-fin rays	11	11 (11)	11 (7)	11 (29) or 12 (1)	11	11
Pectoral-fin rays	2+12+7=21	1–2+9–12+7–10 =20–22 (usually 21) (11)	2+10–12+6–9=20–22 (usually 21) (6)	2–3+8–12+6–10 =19–21 (usually 20 or 21) (27)	?+?+9=20	2+12+7=21
Branched caudal-fin rays	—	9–10 (usually 10) (9)	9–10 (3)	9–10 (24)	—	10
Pored lateral-line scales (LLS)	32	33–39 (10)	33–35 (7)	34–39 (23)	34	34
Anterior LLS with spine	4	3–7 (11)	3–5 (7)	2–8 (usually 3) (28)	4	3
Scale rows above lateral line slanting downward and backward	—	— (0, all damaged)	34–36 (5)	35–40 (15)	35	—
Gill rakers	1+4=5	1+4–5=5 (7) or 6 (4)	1+4–5=5 (4) or 6 (3)	1+4–5=5 (19) or 6 (5)	1+4=5	1+4=5
Lachrymal spines [left (L)/ right (R)]	2/2	2–3 (usually 2) (11)/ 2 (11)	2 (6) or 4 (1)/2–4 (7)	2–3 (24)/2–5 (24) (usually 2/2)	2/2	2/2
Preocular spines (L/R)	2/1	1–3 (11)/1–3 (11) (usually 1/1)	1–4 (7)/1–4 (7)	1–6 (31)/1–6 (31)	3/2	2/1
Suborbital spines (L/R)	18/18	17–24 (11)/16–25 (11)	16–30 (7)/15–29 (7)	14–28 (30)/14–29 (29)	21/22	20/21
Pterotic spines (L/R)	5/5	4–6 (11)/4–7 (11)	3–8 (7)/2–6 (7)	3–10 (31)/3–11 (31)	6/6	4/4
Proportional measurements (% SL):						
HL	44.7	41.7–44.0 (11)	42.1–44.5 (7)	41.6–45.6 (31)	42.8	42.5
Predorsal length	42.6	39.7–42.8 (11)	40.5–43.2 (7)	39.8–44.8 (24)	42.5	41.7
Length of first dorsal-fin base	20.2	20.0–22.6 (11)	19.8–24.6 (7)	18.5–24.7 (27)	21.9	21.9
Length of second dorsal-fin base	24.1	24.1–26.7 (11)	23.4–26.1 (7)	22.8–27.3 (24)	24.4	25.8
Length of anal-fin base	27.4	25.8–28.7 (11)	26.1–27.2 (7)	23.3–29.2 (24)	28.1	27.1
Snout length	11.2	10.7–11.7 (11)	10.5–12.3 (7)	10.9–12.7 (25)	10.4	10.9
Orbital diameter	14.3	13.1–14.2 (11)	12.8–14.8 (7)	12.2–14.8 (25)	14.7	13
Upper jaw length	17.6	16.6–17.6 (11)	16.9–18.4 (7)	16.2–18.7 (25)	17.9	16.5
Lower jaw length	24.1	22.4–23.7 (11)	23.0–25.1 (6)	22.4–26.3 (25)	24.4	22
Interorbital width	2.4	2.0–3.0 (11)	2.3–3.0 (7)	1.6–2.8 (25)	2.2	2.6
Pectoral-fin length	19.9	17.5–19.8 (10)	17.3–18.6 (4)	16.6–19.9 (24)	—	18.6
Pelvic-fin length	—	28.6–31.2 (11)	27.1–30.3 (5)	26.9–32.3 (24)	29.6	30.5
Caudal-fin length	—	22.5–26.2 (10)	22.3–24.1 (3)	22.8–26.6 (23)	—	23.8
Proportional measurements (% HL):						
Snout length	25.1	25.6–27.0 (11)	24.3–27.9 (7)	24.8–28.5 (25)	24.4	25.6
Orbital diameter	32.1	30.2–32.6 (11)	30.2–33.3 (7)	28.2–34.7 (25)	34.3	30.5
Upper jaw	39.5	38.1–40.7 (11)	39.0–41.9 (7)	38.8–42.5 (25)	41.9	38.9
Lower jaw	53.9	52.7–54.6 (11)	52.9–56.3 (6)	53.0–58.5 (25)	57	51.9
Interorbital width	5.3	4.7–7.1 (11)	5.2–7.2 (7)	3.6–6.4 (25)	5.2	6.1

Numbers in parentheses indicate numbers of examined specimens.

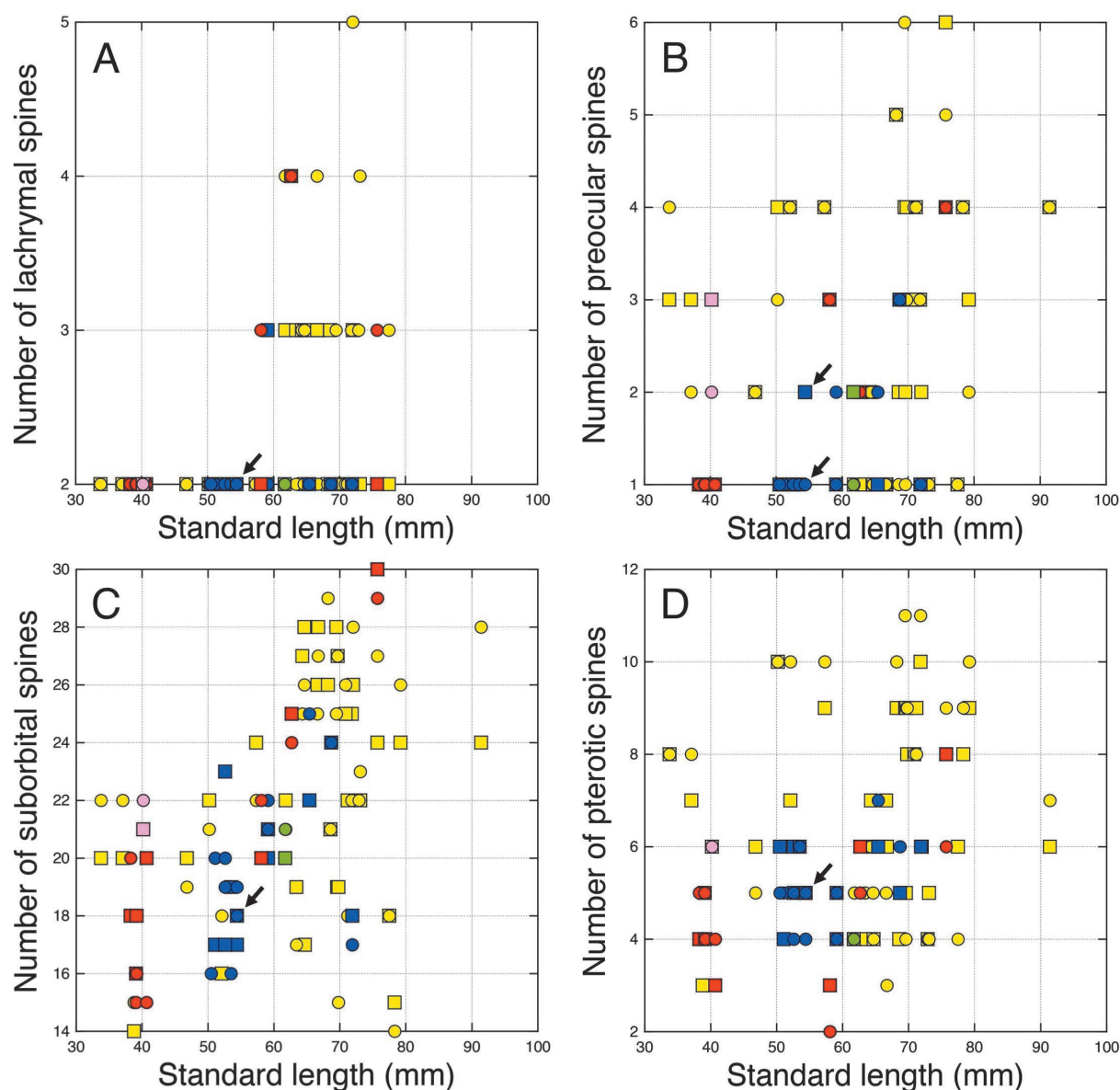


Fig. 3. Comparison of numbers of head spines from five areas and standard length in *Onigocia grandisquama*. A, lachrymal spines; B, preocular spines; C, suborbital spines; D, pterotic spines. Squares, left side of head; circles, right side of head. Arrows indicate holotype values. Colors of symbols represent specimens from the color-coded localities in Figure 2.

Pectoral-fin rays (Table 2).—The number of pectoral-fin rays ranged from 20 to 22 in specimens from the Indian Ocean and from 19 to 21 in those from the western Pacific Ocean. Because the modes of the two ranges also differed from each other (21 in the Indian Ocean vs 20 in the western Pacific Ocean), it can be assumed that the difference has a genetic basis, although specimens with 22 pectoral-fin rays may be found in the western Pacific Ocean in the future. However, as no other remarkable differences between specimens from the two oceans were recognized, I regard this difference as an expression of geographic variation within the species. This is the first record of geographic variation in fin ray counts reported for any platycephalid species.

Lachrymal spines (Figs 3A, 4).—The number of lachrymal spines has been reported as two or three (usually two) in previous studies (Imamura and Sakashita 1997; Imamura and McGrouther 2008). The present study revealed the

Table 2. Frequency of pectoral-fin ray counts in *Onigocia grandisquama* from five regions.

	19	20	21	22
Western Indian Ocean ($n=12$)		2	8*	2
Eastern Indian Ocean ($n=6$)		2	3	1
Coral Sea ($n=27$)	1	16	10	
Ceram Sea ($n=1$)		1		
Gulf of Thailand ($n=1$)			1	

*Including holotype

variation to be from two to five (including small spines), with a tendency for spine number to increase with growth as follows: only two spines were observed in specimens of 33.8–57.3 mm SL; the third, fourth, and fifth spines were first seen in specimens of 58.1 mm SL (WAM P. 28754-009, right side only), 66.6 mm SL (QM I. 40097, right side only),

and 72.0 mm SL (QM I. 37839, right side only), respectively. Still, specimens with only two spines were present at most body sizes.

Preocular spines (Figs 3B, 4).—Although one or two (usually two) preocular spines have been known in this species (Imamura and Sakashita 1997; Imamura and McGrouther 2008), this study found that the number of spines varied from one to six. Change with growth was also observed, with larger specimens tending to have more spines, although the smallest specimen examined (QM I. 37297, 33.8 mm SL) has just three (left) and four (right) spines. In addition, as with the lachrymal spines, specimens with only one preocular spine were found at most body sizes.

Suborbital spines (Figs 3C, 4).—Although species of *Onigocia* have been known to have a serrated suborbital ridge (e.g., Imamura 1996), most authors have not paid attention to the number of small spines on it. This study

found the number of suborbital spines to be greatly variable in *O. grandisquama*, ranging from 14 to 30 and tending to increase with growth.

Some specimens of moderate to large size have fewer suborbital spines than other, similarly sized fish of *Onigocia*, and with wider interruptions of the serration that differ from the typical condition for *O. grandisquama* of mostly continuous serration. However, the suborbital spine number serially varied among the 52 examined specimens and could not be clearly separated into any distinct groups. I conclude that the variation in spine number represents intraspecific variability.

Pterotic spines (Figs 3D, 4).—Although the number of pterotic spines has not been used previously to separate species of *Onigocia*, this study revealed that this feature distinguishes *O. grandisquama* from several congeners to some degree (see discussion under Comparison below for details).

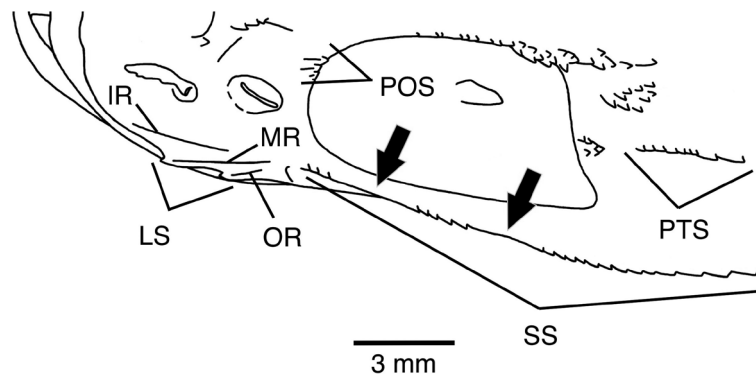


Fig. 4. Dorsal view of left side of head of *Onigocia grandisquama*, QM I. 37414, 71.2 mm SL. IR (inner), MR (middle), and OR (outer) ridges on lachrymal; LS, lachrymal spines; POS, preocular spines; PTS, pterotic spines; SS, serration on suborbital ridge. Arrows indicate interruptions of serration on suborbital ridge.

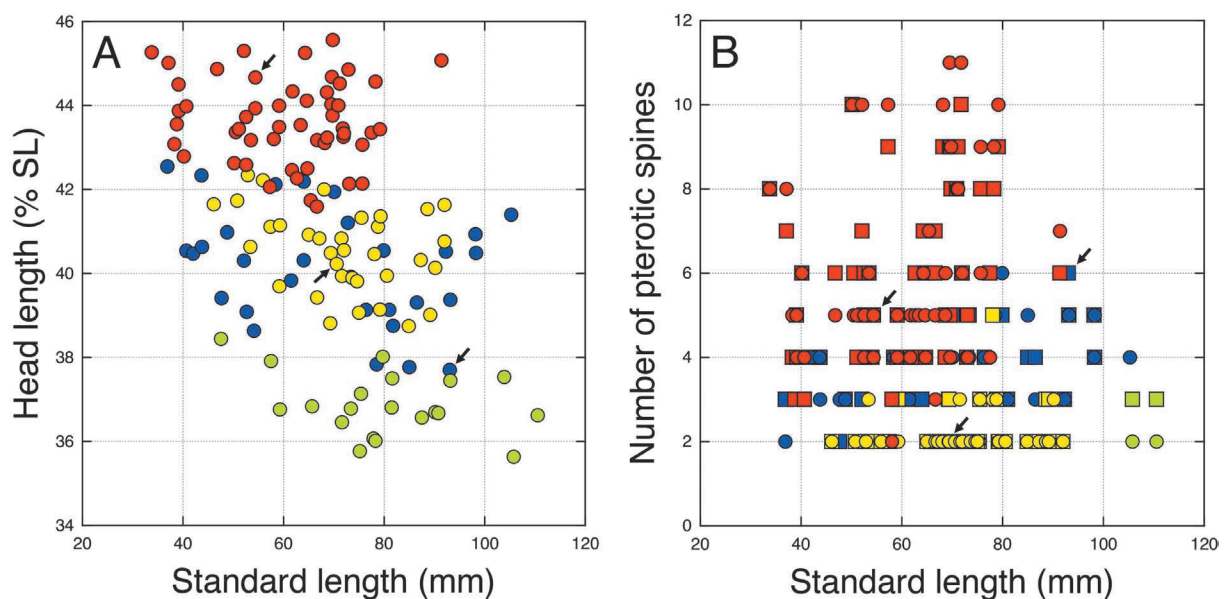


Fig. 5. Comparison of head length (A) and number of pterotic spines (B: square, left side; circle, right side), with standard length in four species of *Onigocia* with an ocular flap. Red, *O. grandisquama*; yellow, *O. macrocephala*; green, *O. macrolepis*; blue, *O. spinosa*. Arrows indicate holotype or lectotype specimens.

Table 3. Comparison of selected characters between *Onigocia grandisquama* and eight congeners.

	<i>O. grandisquama</i> (<i>n</i> = 52 ^b)	<i>O. spinosa</i> (<i>n</i> = 30)	<i>O. macrocephala</i> (<i>n</i> = 34 ^a)	<i>O. macrolepis</i> (<i>n</i> = 19)	<i>O. bimaculata</i> (<i>n</i> = 11 ^b)	<i>O. lacrimalis</i> (<i>n</i> = 13 ^b)	<i>O. oligolepis</i> (<i>n</i> = 1 ^b)	<i>O. pedimaculata</i> ^a Holotype	<i>O. pedimaculata</i> ^a Others (<i>n</i> = 12)	<i>O. sibogae</i> (<i>n</i> = 20)
SL (mm)	33.8–91.4	36.9–105.3	46.1–92.0	47.6–110.6	23.2–74.6	54.6–143.7	82.2	49.1	31.0–92.0	39.1–70.9
First dorsal-fin rays	I+VII or VIII (usually VIII)	I+VII–IX (usually VIII)	I+VII or VIII (usually VIII)	I+VII or VIII (usually VIII)	I+VII or VIII	I+VII or VIII	I+VIII	I+VIII	I+VIII	I+VII or VIII (usually VII)
Second dorsal-fin rays	10–11 (usually 11)	11–12 (usually 12)	10–12 (usually 11)	11–12	11	12–13 (usually 12)	11	11	10–12 (usually 11)	11–12 (usually 11)
Anal-fin rays	11–12 (usually 11)	11–13 (usually 12)	11–12 (usually 12)	12–13 (usually 12)	10–11 (usually 11)	12	11	11	11–12 (usually 11)	10–11 (usually 11)
Pectoral-fin rays	19–22 (usually 20–21)	20–22 (usually 21)	21–23	19–22 (usually 20–21)	19–22 (usually 11)	21–25	22	21	20–22	19–21
Branched caudal-fin rays	9–10	9–10	9–10	9–11	7–9 ^c	8	—	8	8	8
Pored lateral line scales (LLS)	32–39	35–41	32–39	36–42	35–38	32–35	32	31	30–33	30–31
Anterior LLS with spine	2–8	7–20	3–11	2–5	2–8 (usually 3)	2–4 (often 3)	3	3	3–9 (usually 3)	2–3 (usually 3)
Gill rakers	1+4–5=5–6 (usually 5)	1+4–5=5–6 (usually 5)	1+4–6=5–7 (usually 6)	1+3–5=4–6 (usually 5)	1+4–7=5–8 (usually 7)	0+4–5=4–5	1+4=5	0+4=4	0–1+4–7=4–7	0–1+4–5=4–5 (usually 0+4=5)
Lachrymal spines ^d	2–5	2–10 (usually 3 or more)	2–9	2–3 or 2 plus short serration (usually 2)	2–7 (usually 2)	0–1 (usually 0)	2	2	2–3 (usually 2)	2–3 (usually 2)
Preocular spines	1–6	2–6	1–2 (usually 1)	1	1–5	1	3	4	2–5	2–5
Pterotic spines	3–11	2–6	2–5 (usually 2)	2–3 (usually 2)	3–6	2–6	2–3	4–5	2–5	2–5 (usually 2 or 3)
HL (% SL)	39.4–45.6	37.7–42.5	38.8–42.3	35.6–38.4	33.8–39.3	39.3–42.6	41.0	40.7	37.1–41.6	38.6–43.5
Ocular flap on posterior portion of eye	Present	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Small and short papillae on posteromedial portion of eye	Absent	Absent	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Upper iris lappet	Short and branched	Short and branched	Short and branched	Short and branched	Simple or bilobed	Scalloped, bilobed, or absent	Weakly bilobed	Simple	Scalloped or trilobed	Usually finely crenate, rarely absent
Notch on suborbital ridge below eye	Absent	Present	Present	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Interopercular flap	Absent	Absent	Absent	Absent	Present	Absent	Absent	Absent	Absent	Absent
Distinct spot(s) on pelvic fin	Absent	Absent	Absent	Absent	One spot basally, often 2–3 blotches or bars distally	Absent	Unknown	One large spot	Absent	2–4 spots

^aThe holotype from the eastern Indian Ocean and non-types from the western Pacific are shown separately because Imamura (2011) pointed out that the latter may be a different species^bIncluding holotype or lectotype^cSmaller specimens with fewer rays (7 in 26.2 mm SL or smaller; 8 in 36.8 mm SL, 9 in 42.3 mm SL or larger)^dIncluding small spines

Pterotic spine numbers varied from two to 11 in the specimens examined, with usually four or more present and with the number tending to increase with growth.

Comparison. Data used for the following comparison are from Knapp (1999), Imamura and McGrouther (2008), Imamura and Knapp (2009), Imamura (2011, 2012), and this study.

In addition to *O. grandisquama*, the genus *Onigocia* includes the following eight valid species at present: *Onigocia bimaculata* Knapp, Imamura, and Sakashita, 2000, *Onigocia lacrimalis* Imamura and Knapp, 2009, *Onigocia macrocephala* (Weber, 1913), *Onigocia macrolepis* (Bleeker, 1854), *Onigocia oligolepis* (Regan, 1908), *Onigocia pedimacula* (Regan, 1908), *Onigocia sibogae* Imamura, 2011, and *O. spinosa* (see Imamura 2012). *Onigocia grandisquama* is easily separable from *O. bimaculata*, *O. lacrimalis*, *O. oligolepis*, *O. pedimacula*, and *O. sibogae* in having 9–10 branched caudal-fin rays, an ocular flap on the posterior part of the eye, and a short and branched upper iris lappet (vs. eight branched caudal-fin rays, no ocular flap, and an upper iris lappet that is variously bilobed, trilobed, scalloped, crenate, or absent in the others). The holotype of *O. oligolepis*, the sole specimen of that species examined here, has a broken caudal fin, which makes its ray number uncountable.

Among *O. macrocephala*, *O. macrolepis*, and *O. spinosa*, which share the three above-mentioned characters with *O. grandisquama*, *O. spinosa* most closely resembles *O. grandisquama* in lacking a notch on the suborbital ridge below the eye (vs. notch present in *O. macrocephala* and *O. macrolepis*). Knapp (1999) described *O. spinosa* as having XI total first dorsal-fin spines, 11 or 12 (usually 12) second dorsal-fin rays, 11 or 12 (usually 12) anal-fin rays, 34–42 pored lateral-line scales, the anterior 7–27 scales each with a spine or ridge, five or six total gill rakers, three lachrymal spines, and three to five preocular spines, all values that mostly or partly overlap those of *O. grandisquama*. In addition, two specimens of *O. spinosa* examined in the present study have two lachrymal spines, and one of them (NTM S. 15848-001, 48.8 mm SL) also has 11 second dorsal- and anal-fin rays, a spine on each of the anterior seven lateral-line scales, and three or four preocular spines, all of which overlap with the counts of *O. grandisquama*. Accordingly, this specimen cannot be separated from *O. grandisquama* using the characters, which were previously considered useful for separating the two species.

The present study, however, revealed a valuable feature that does separate *O. grandisquama* and *O. spinosa*, the presence or absence of spines on the inner, middle, and/or outer ridges on the lachrymal. In *O. grandisquama*, spines are absent on these ridges even in larger specimens (Fig. 4), while spine(s) are present at least on the inner ridge in *O. spinosa* at lengths of 48.8 mm SL or more [an even smaller specimen (NSMT-P 53253, 40.7 mm SL) from Nagasaki, Japan, also has a spine on the inner ridge], and tend to increase in number with growth and to develop from the inner to outer ridges [for example, CSIRO CA 1876 (64.0 mm SL) has three, two, and no spines on the inner, middle, and outer ridges, respectively, on the left side, and CAS 15237

(98.3 mm SL) has five, five, and two spines on the right side]. Accordingly, the presence or absence of the spines is useful for separating specimens of these two species above a certain size. In addition, this difference also distinguishes *O. grandisquama* from *O. macrocephala* and *O. macrolepis*, which usually have the spines (although they are absent in smaller specimens of the latter two species and in a few larger specimens of *O. macrocephala*), supplementing the above-mentioned presence or absence of a notch on the suborbital ridge below the eye. Head length is also valuable for separating *O. grandisquama* from *O. spinosa*, *O. macrocephala*, and *O. macrolepis* (41.6–45.6% SL in *O. grandisquama* vs. 37.7–42.5% SL in *O. spinosa*, 38.8–42.3% SL in *O. macrocephala* and 35.6–38.4% SL in *O. macrolepis*), although there is some overlap between *O. grandisquama*, and *O. spinosa* and *O. macrocephala* (Fig. 5A). As was mentioned above, the number of pterotic spines in *O. grandisquama* varies from two to 11, and is usually four or more. Although these numbers do not clearly distinguish *O. grandisquama* from the three species with an ocular flap, they help to separate them, as there are generally fewer pterotic spines in the latter species, especially in *O. macrolepis*: two to six (tending to increase with growth) in *O. spinosa*, two to five (usually two) in *O. macrocephala*, and two to three (usually two) in *O. macrolepis* (Fig. 5B).

Characters capable of separating *O. grandisquama* from other congeners, including some not discussed here, are summarized in Table 3.

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