REVIEW OF THE GENUS *PHOToblepharon* (ACTINOPTERYGII: BERYCIFORMES: ANOMALOPIDAE)

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Abstract. The flashlight fishes of the genus *Photoblepharon* (Family: Anomalopidae) are herein reviewed, in order to clarify their taxonomy. The genus includes two species *Photoblepharon palpebratum* (Boddaert, 1781) from the eastern Indian Ocean and the western Pacific Ocean and *Photoblepharon steinitzi* Abe et Haneda, 1973 from the Red Sea, Oman, and western Indian Ocean. The study was initiated because the holotype of *P. steinitzi* was lost. Neotypes for these two species are designated due to the loss of the type specimens of both species and problems with the identity of the two species. A key for these species is provided. Several biological, ecological and other uses of the light organ are given for *P. steinitzi* from the Gulf of Aqaba. Observations in nature and experiments in the aquarium are described.

Keywords: flashlight fish, *Photoblepharon palpebratum*, *Photoblepharon steinitzi*, taxonomy

INTRODUCTION

The flashlight fishes of the family Anomalopidae are a group of marine fishes characterized by a large luminous organ which is situated below the eye, with a rotational and/or shutter mechanism for controlling light emission (Nelson 2006). They are distributed in warm waters of the Indo-West Pacific, the eastern Pacific, and the western Atlantic. The family comprises 6 genera with 9 species (Nelson 2006, Ho and Johnson 2012).

The genus *Photoblepharon* was first described by Weber (1902) for the western Pacific *Sparus palpebratus* Boddaert, 1781, a species of flashlight fish with a single dorsal fin and a fixed (not rotating) luminous organ. Abe and Haneda (1973) added a new subspecies, *P. palpebratus steinitzi*, which was later raised to species level by McCosker and Rosenblatt (1987), who reviewed the family and found several distinguishing characters between the two species, including the pelvic-fin ray number, the number of spinules on the posterior margin of the maxilla, and the colouration of the opercle.

However, there has been some confusion concerning the identity of the two species in the literature, and both species are devoid of type specimens. The purpose of this current paper is to review the species of *Photoblepharon*, and to stabilize the prevailing usage of the species names *Sparus palpebratus* Boddaert, 1781 and *Photoblepharon steinitzi* Abe et Haneda, 1973 (in the sense of McCosker and Rosenblatt 1987) by neotype designations.

METHODS

Count and measurement methods follow McCosker and Rosenblatt (1987). The last soft ray in the dorsal and anal fin is split at its base, but counts as a single ray. The standard length is abbreviated SL, the head length HL. Collection acronyms follow Fricke and Eschmeyer (2018).

The following abbreviations were used: the Natural History Museum, London, UK (BMNH), the California Academy of Sciences, San Francisco, USA (CAS), the Hebrew University Fish Collection, Jerusalem, Israel (HUJ), the Steinhart Museum of Natural History, Tel Aviv University, Tel Aviv, Israel (SMNHTAU), the Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS), and the University Museum, University of Tokyo, Tokyo, Japan (ZUMT).

**Comparative material.** *Anomalops katoptron* (Bleeker, 1856): BMNH 1890.9.1.8 (1), Vanuatu; SMNS 24078 (1), Philippines, Mindanao.
RESULTS

Family ANOMALOIDAE

Photoblepharon Weber, 1902

Photoblepharon Weber, 1902; Weber 1902: 108 (type species: Sparus palpebratus Boddart, 1781; type by monotypy), Weber and de Beaufort 1929: 226, McCosker and Rosenblatt 1987: 158, Johnson and Rosenblatt 1988: 71, Rosenblatt and Johnson 1991: 333, Kotlyar 1996: 214, Baldwin et al. 1997: 377, Paxton and Johnson 1999: 2213, Paxton et al. 2006: 764.

Diagnosis. Moderately deep body with slightly rounded dorsal and ventral contours. Rather long caudal peduncle. Blunt head with short snout. Anterior and posterior nostrils close to each other. Eyes large; elliptical light organ under eye, which cannot be rotated ventrally into pocket, but with black shutter that lifts to cover organ. Lateral line slightly arched above pectoral fin. Dorsal fin single, triangular, with 2 small spines and 17–19 rays. Anal fin with 2 small spines and 14–15 rays. Caudal fin forked. Pectoral fin with 16–18 rays and pelvic fin with 6–7 rays.

Key to the species of Photoblepharon Weber, 1902

1a. Conspicuous white spot at upper corner of opercle, covering naked area; pelvic-fin rays 7; rear tip of maxilla heavily sculptured with 23 or more small denticles.........................................................
1b. Naked area at upper corner of opercle with a small elongate, not obvious white spot; pelvic-fin rays 6; rear tip of maxilla sculptured with 18 or less small denticles...............................................................
closed. Small shallow knob-like bulge on anterior of upper jaw with small teeth spaced at symphysis. At the anterior of lower jaw knob-like enlargement with larger teeth having gap at symphysis, visible when mouth is closed, followed by narrow bands of small teeth arranged in irregular rows. Rear tip of maxilla sculptured with 25 denticles. Eye large, its horizontal diameter 41.4% of HL. Under eye is an elliptical light organ, its length 47.5% of HL and depth 15.6% of HL. Gill rakers 5 + 16. Lateral line slightly arched above pectoral fin; lateral-line scales 34. Dorsal fin triangular, with 2 small spines and 19 rays, 6th–8th rays being longest. Anal fin with 2 small spines and 14 rays, 4th ray being longest. Caudal fin forked. Pectoral fin with 18 rays and pelvic fin with 7 rays.

**Colouration.** Randall et al. (1997: 498) and Laboute and Grandperrin (2000: 150; 2016: 166) provided colour photographs of live specimens. Body and fins are blackish. Lateral line and the posterior edge of operculum white to light blue. Large white spot on dorsal corner of opercle. The light organ is white. Colour of the preserved neotype is light brown, the pectoral fin dark brown, white

![Fig. 1. Photoblepharon palpebratum (Boddaert, 1781), neotype, CAS 82480, 72.6 mm SL, Banda Sea, Indonesia, Maluku, Pulau Lucipara (Photograph: D. Golani)](image1)

![Fig. 2. Geographical distribution of Photoblepharon palpebratum (A) and Photoblepharon steinitzi (B)](image2)
spot on dorsal corner of opercle. The light organ is white surrounded by black tissue (Fig. 1).

**Distribution.** Christmas Island; Ryukyu Islands (Okinawa); Indonesia (Kalimantan; Bali; Flores; Maluku: Banda, Pulau Lucipara, Ambon; West Papua), Malaysia (Sabah), Philippines (Cebu; Mindoro), Mariana Islands, Palau, Federated States of Micronesia (Orolock, Caroline Islands), Marshall Islands (Kwajalein; Eniwetok), Papua New Guinea (Madang; Port Moresby), Australia (Queensland; Coral Sea Islands Territory), New Caledonia (Grand Terre), Kiribati (Phoenix Islands), Cook Islands (Rarotonga) (Fig. 2).

**Remarks.** Boddaert (1781) described *Sparus palpebratus* based on two specimens, one in the collection of Gaubius, the other in his own collection, said to occur near Amboina (Ambon, Indonesia). One of the specimens had no locality, the other locality was doubtful, as at the time specimens were collected by sailors or medical doctors from fish markets throughout the region, and brought to the Netherlands on tedious voyages where they could easily have been mixed up and confused, for example with material from the Mascarenes. The description of *Sparus palpebratus* is insufficient to distinguish between the two species of the genus or the co-occurring *Anomalops katoptron* (Bleeker, 1856), and the plate is not available in any of the three online versions of volume 2 of the Neue Nordische Beyträge zur physikalischen und geographischen Erd- und Völkerbeschreibung, Naturgeschichte und Oekonomie we could detect, so it may not have been published. The six pelvic fin rays described by Boddaert (1781) rather point to *Photoblepharon steinitzi* than to *P. palpebratus*. The authors of the Catalog of Fishes online (Fricke et al. 2018) have been unable to detect any of the two syntypes over a period of nearly 40 years of intensive search of fish types, so they are considered to be lost. In order to stabilize the present usage of the name *Photoblepharon palpebratum* (Boddaert, 1781), we hereby designate the specimen CAS 82480 (described above) as the neotype of *Sparus palpebratus* Boddaert, 1781. The neotype originates from the Lucipara Islands in the Banda Sea, which are as close as possible to the assumed original type locality.

A record of *Anomalops katoptron* (non Boddaert, 1781) of Ogilby (1890: 70, Vanuatu) and Reuvens (1897: 127, Sulawesi, Indonesia) is based on misidentified specimens of *Anomalops katoptron* (Bleeker, 1856); this misidentification is confirmed by the authors who re-examined one of the specimens used by Ogilby (BMNH 1890.9.1.8, collected in the Bay of Bengal according to the label, but in Vanuatu according to the BMNH fish catalogue entry).

*Photoblepharon steinitzi* Abe et Haneda, 1973 (Fig. 3)

*Photoblepharon* sp.: Fridman 1972: 1.

*Photoblepharon palpebratum steinitzi* Abe et Haneda, 1973; Abe and Haneda 1973: 57, Godeaux 1979: 169, fig. 8, Bauchot et al. 1982: 390, Scharzhans 1980: 110, fig. 358 (otolith), McCosker 1986: 413 (Grand Comoro Island), Fricke 1999: 125 (Réunion), Letourneur et al. 2004: 209. *Photoblepharon palpebratus* (non Boddaert, 1781): McCosker and Lagios 1975: 1, Morin et al. 1975: 74, Randall 1983: 36, Debelius 1999: 60.

*Photoblepharon palpebratum steinitzi*: Dor 1984: 70, Debelius 1993: 63, Fricke 1999: 125. *Photoblepharon palpebratum steinitzi*: McCosker and Rosenblatt 1987: 161 (Israel; Egypt; Grande Comore Island), Randall and Anderson 1993: 9 (Maldives), Goren and Dor 1994: 17, Randall, 1995: 93 (southern Oman), Kotlyar 1996: 216, Randall et al. 1997: 498, Debelius 1998: 32 (Sharm el Sheikh, Egypt), Manilo and Bogorodsky 2003: S100, Lieske and Myers 2004: 49 (Movenpick Resort, Soma Bay, Egypt), Randall 2005: 85, Fricke et al. 2009: 32, Golani and Bogorodsky 2010: 18, Hellinger et al. 2017: 2, Jawad et al. 2018: 71, fig. 1.

**Neotype.** (as designated below): HUJ 20546, 66.6 mm SL, Gulf of Aqaba, 1975.

**Other material examined.** BMNH 1875.12.8.1, 1 specimen, 73.3 mm SL, Comoros, Grande Comore Island, north of Itsandra, 11°39′19″S, 43°15′42″E, J.E. McCosker, 16 Feb. 1975; CAS 35113, 1 specimen, 65.3 mm SL, Comoros, Grande Comore Island, north of Itsandra, 11°39′19″S, 43°15′42″E, J.E. McCosker, 16 Feb. 1975; HUJ 20550, 2 specimens, 66.7, 68.6 mm SL, Gulf of Aqaba, 1975; SMNIHTAU 7059, 61.2 mm SL, Eilat, Gulf of Aqaba. 20 Nov. 1972.

**Diagnosis.** Body moderately deep, body depth 34.8%–47.9% of SL. Caudal-peduncle length 21.6%–32.7% of SL, caudal-peduncle depth 12.1%–13.6% of SL. Head length 33.2%–38.0% of SL, snout length 12.9%–16.3% of HL. Anterior and posterior nostrils close to each other, situated at level of upper three quarters of orbit. Dorsal profile of head slightly convex. Rear tip of maxilla sculptured with 11–18 denticles. Eye large, its horizontal diameter 38.4%–44.6% of HL. Light organ elliptical, its length 43.8%–52.1% of HL, it depth 14.6%–18.3% of HL. Gill rakers 5 + 17–22. Lateral line slightly arched above pectoral fin; lateral-line scales 31–34. Dorsal fin triangular, with 2 small spines and 16–18 rays, 6th–8th rays being longest. Anal fin with 2 small spines and 13–15 rays, 3rd ray being longest. Pectoral fin with 16–17 rays and pelvic fin with 6 rays.

**Description of the Neotype.** Moderately deep body (34.8% of SL) with slightly rounded dorsal and ventral contours. Rather long caudal peduncle, its length 21.6% of SL and its depth 12.9% of SL. Blunt head, head length 43.8%–52.1% of HL, it depth 14.6%–18.3% of HL. Gill rakers 5 + 17–22. Lateral line slightly arched above pectoral fin; lateral-line scales 31–34. Dorsal fin triangular, with 2 small spines and 16–18 rays, 6th–8th rays being longest. Anal fin with 2 small spines and 13–15 rays, 3rd ray being longest. Pectoral fin with 16–17 rays and pelvic fin with 6 rays.
Review of the genus *Photoblepharon*

32. Dorsal fin triangular, with 2 small spines and 17 rays, 6th–8th rays being longest. Anal fin with 2 small spines and 14 rays, 3rd ray being longest. Caudal fin forked. Pectoral fin with 16 rays and pelvic fin with 6 rays. **Colouration.** Randall (1983: 36), Debelius (1998) and Lieske and Myers (2004) provided colour photographs of live specimens. Body and fins are blackish. Lateral line and the posterior edge of operculum light blue. Small, elongate white spot at upper corner of opercle. The light organ is white. Margins of dorsal, anal and caudal fins bright blue, leading edge of pelvic fins bright blue. Colour of the preserved neotype is light brown, the pectoral fin dark brown. The light organ is white surrounded by black tissue (Fig. 1).

**Distribution.** Red Sea (Gulf of Aqaba: Israel, Egypt; El-Qusayr, Egypt), Oman (south coast), Comoros (Grande Comore), Réunion, Maldives (Fig. 2).

**Remarks.** In 1973, Abe and Haneda described *Photoblepharon palpebratus steinitzi*, as a new subspecies of flashlight fish from the Gulf of Eilat (Gulf of Aqaba), Red Sea, based on three specimens, all from the Hebrew University Fish Collection (HUJ). The holotype was HUJ-F 5368a and the paratypes were HUJ-F 5131 and HUJ-F 5368b. Several years later, Randall (1983) did not agree with the division into two subspecies. However, even later McCosker and Rosenblatt (1987) agreed with Abe and Haneda (1973) and elevated *Photoblepharon steinitzi* to the specific level, based on the different number of pelvic fin rays, the shape of the sculpturing on the rear tip of the maxilla and the supramaxilla and some colour patterns.

Since the 1980s one of the authors (D.G.) has tried to locate the three types specimens, to no avail. This led to the conclusion that the type specimens have been lost (Golani 2006: 23). The second author (R.F.) also enquired about materials, which were sent on loan to the late T. Abe (ZUMT), and was informed by K. Mochizuki (personal communication, 1998) that unfortunately these materials were lost (for a biography of T. Abe see Arai 1997). McCosker and Rosenblatt (1987) identified some western Indian Ocean populations as *P. steinitzi*, while eastern Indian Ocean populations were attributed to *P. palpebratum*. Apparently erroneously, Debelius (1999) restricted *P. steinitzi* to the Red Sea and considered the Indian Ocean populations as *P. palpebratum* (non Boddaert, 1781).

*Photoblepharon steinitzi* is characterised by the pelvic fin rays usually I, 5 (versus usually I, 6 in *P. palpebratum*), and the anteriormost lateral-line pore preceded by a small, not obvious white spot on dorsal corner of opercle (versus preceded by a bright white spot on dorsal corner of opercle in *P. palpebratum*).

The specimen HUJ 20546 (66.6 mm SL, see Fig. 3) is hereby designated as the neotype of *Photoblepharon steinitzi* Abe et Haneda, 1973 (see the remarks above).

The original holotype (HUJ F5368a) was collected at Ras Burqa [near Nuweiba], Gulf of Aqaba, Red Sea. The neotype likewise originates from the Gulf of Aqaba, Red Sea.

**DISCUSSION**

The biology and ecology of the species of the genus *Photoblepharon* have fascinated researchers for many years. Like other members of the family, *P. steinitzi* is a nocturnal species, active mainly on moonless nights. During the day, it hides in caves and crevices, usually in small groups, up to 100 fish, at depths of 50 m to the surface (Fridman 1972). *Photoblepharon steinitzi* is equipped with a bean-shaped luminous organ under each eye. The light is produced by symbiotic bacteria, which are species-specific, as a result of a metabolic process (McCosker 1977). The manner in which the newly hatched fish acquire the symbiotic bacteria is not clear. All attempts to extract and culture the bacteria have failed. Nevertheless the bacteria continue to glow several hours after removal from the fish. The light organ can be switched off by pulling a black membrane over it (McCosker 1977). The light organ and the ability to turn it off serve the fish for several purposes. The light attracts various organisms, mainly zooplankton; this phenomenon

![Photoblepharon steinitzi](image)

*Fig. 3. Photoblepharon steinitzi* Abe et Haneda, 1973, neotype, HUJ 20546, 66.6 mm SL, Gulf of Aqaba (Photograph: D. Golani)
is known as phototactism. *Photoblepharon steinitzi* feeds mainly on Mysidacea, Cumacea, Amphipoda, and, to a lesser extent, fish larvae, polychaetes and some benthic crustaceans, their proportion in stomach contents was much higher than in the environment (Sagi unpublished). Sagi (unpublished*) reported a series of experiments on *Photoblepharon* in aquaria and showed that they prey selectively.

The switching on and off of the light organ also assists the fish in escaping predators. When threatened, the fish moves in a zigzag pattern, while flashing its light, which confuses the predator (Clark 1978). In addition, the blinking of several fish coordinated in a group distracts the predator and makes it difficult to concentrate on specific individual fish (McCosker 1977). The rate of blinking the light organ on and off also constitutes communication between fishes including intra-specific recognition and searching for a potential mate (Sagi unpublished)

The light organ is apparently fully developed in adult specimens only; larvae of the Atlantic Ocean species *Kryptophanaron alfredi* Silvester et Fowler, 1926 are lacking an obvious light organ (Baldwin and Johnson 1995). McCosker (1982) reported an allometric growth of the light organ relative to the head length in subadult and adult specimens of anomalopids. Though larvae and juveniles of the genus *Photoblepharon* are still unknown, the size and allometric growth might be similar in that genus.

The spawning season of *Photoblepharon steinitzi* in the Gulf of Aqaba extends from July to September. Each batch consists of ca. 600 eggs; most likely there are several batches per spawning season (Sagi unpublished). The larvae have a quite brief planktonic stage of 12–14 h. Juveniles inhabit rocky substrate or hide near corals, mainly of the genus *Acropora*. The juveniles join the group only after reaching adult size (Sagi unpublished). The smallest specimen collected in the Gulf of Aqaba was 10 mm and externally had an adult shape with a complete and presumably functioning light organ.

Six individuals of *Photoblepharon steinitzi* are kept in the Underwater Observatory Marine Park in Eilat, Israel; some of these have been there for at least 20 years. Two of these fish have ceased to have functioning light organs (A. Levi, personal communication).

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