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The Source of Light in the Luminous Fishes, *Anomalops* and *Photoblepharon*, from the Banda Islands

Y. HANEDA* and F. I. TSUJI**

(With 3 Text-figures and 1 Plate)

バンダ島の2種の発光魚*Anomalops* と *Photobrepharon*

羽根田弥太*　フレデリック辻一郎**

バンダ島はインドネシアのモルッカス群島 (Molucus, Maluku), バンダ海にある小火山島群で，アンボン (Ambon) から135浬の距離にある。中央の富士山形の火山 (Gunung Api. 520米) と小バンダ (Banda kechil), 大バンダ (Banda besar) の間は湖水のように静かで美しい珊瑚礁の海である。古くからニクヅク (Pala, *Myristica fragrans*) の産地として知られこの地方がアンボンと共に香料群島の名で，広く世界に紹介されていた。

この島にはヒカリキンメダイ *Anomalops katoptron* と *Photobrepharon palpebratus* とよぶ2種の発光魚が知られている。両種とも体長 70～80 ミリ暗褐色で，眼の下に，ソラ豆状の淡黄白色の発光器を持っている。前者はバンダ島の他にアンボン，西イリアン，パウモーツス，ニューヘブライデス諸島にも分布し，非常に稀に日本近海でも数尾採集された記録がある。後者はバンダ島の他には，まだ採集された記録はない。

1925年プリンストン大学の教授故ニュートン，ハーヴェイ博士は単身この島をおとづれ，この興味ある2種の魚を研究し，広く世界に紹介した。それ以来実に 50 年の長い間，一人の科学者もこの島を訪れたことがなかった。

私等は 1959 年9月末から 12 月にかけて行なわれたカリフォルニア大学の実験船アルファフェリックス号 (R/V Alpha Helix) による生物発光を目的とするニューギニア探検に参加したのを機会に，多年希望したバンダ島への旅を試みた。ブリスベーンのモートン湾のエビ網舟の漁獲物を調べた後，モルッカス諸島のアンボンに着き，バンダ島への船便を調べたところ，150 トンのアンペラ 1 号 (Ampera Satu) という貨物船が不定期にバンダへ寄ることを知った。そこで辻はニューギニアのマダン基地に帰り，羽根田は 11 月 20 日アンボン出港，翌日夕方，バンダ島に上陸した。バンダ島にはホテルが無いと聞いていたが，アンボン総督秘書デリマ氏 (De Lima)，バンダ島，バンダネイラ町の助役アルブラム氏 (ALI ALBRAM)，警察署長アウグスチン氏 (J. AUGUSTYN) 等の世話でツアパチナヤ氏 (H. J. TUAPATTINAJA) の宅に宿泊，目的の発光魚の採集の手配など，これ等の方々の配慮でなされ，充分な材料をとることができた。

2種の発光魚 *Anomalops* と *Photobrepharon*

この2種の発光魚は，この島では誰知らぬ者もない普通の魚でイカンラウエリ Ikan laweri とよんでいることがわかった。この2種の魚は暗夜にのみ現われ，月夜には深い海か，珊瑚礁の暗いところにかくれているとゆう。島に到着した日は満月の2日前であり，止むなく，数日を待たねばならなか

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We are deeply indebted to messrs. A. Delima and Adolf Hutabarat in Ambon; Ali ALBRAM, J. AUGUSTYN and H. J. TUAPATTINAJA in Banda, having kindly collected materials and for their kindness during Haneda's stay in Banda.

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* Yokosuka City Museum, Yokosuka, Japan.

** Department of Biophysics and Microbiology, University of Pittsburgh, and Veterans Hospital, Pittsburgh, Pennslyvania, U.S.A.

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った。月が落ちてからは毎晩，採集することができた。

Anomalops をインドネシア語でイカンラウエリ，アエル (Ikan 魚，Laweri この魚の固有名詞，Air 水)，*Photobrepharon* をイカン，ラウエリ，バツ (Ikan Laweri Batu 岩) とよび，前者は通常数十尾が群をなし，表層，あるいは数米のところを泳ぐので，夜間，光を目標として，採集しやすいが，後者は水深，5, 6 米の珊瑚礁または溶岩の間を一対ずつ出入しているので採集は困難であった。

両種とも発光器の構造は同じで眼の下の黒色の凹所におさまっている。発光体はソラ豆状で表面は淡黄白色，表面に樹枝状の毛細血管がみられ，裏面は黒色である。このソラ豆状の発光器の前端が軟骨で連絡し，*Anomalops* は発光器を回転して，光を消すときは発光面を黒い膜で完全に包み，*Photobrepharon* では発光器そのものは動かず，ちょうどマブタのような黒色の膜がまばたきをするように下から上へと上り発光面を包むことになる。

光は明暗のない連続的の光で緑青色である。両種共，瓶に入れて，暗い室へ持って行くと，ぱっと光り，明るい室へ持ってくると，直ちに光を消す。魚の死後，発光器の光が急に暗くなることもあるが，生魚の発光器を切りとり，冷しておくと，10時間も光っているのを観察した。この島の漁夫は大きい魚を釣るときに，これ等の魚の発光器を切りとり，餌の上，4, 5 センチのところにつけて，魚を誘引するのに使っている。

カヌーで出漁するときはブブ (Bubu) とよぶ太い竹の飼育器に，生きた魚を 10 尾ほど入れて，このブブを 5, 6 本水中に入れて曳いて行くのが常である。

発光器の内容

発光器内の発光体について，ハーヴェイ (1921) は培養は出来なかったが，発光器内に共生する発光バリテリアであることを主張した。羽根田 (1943, 1953, 1955) は西ニューギニアのアヌクワリ港で採集した 15 ミリの幼魚について発光細菌培養試験を行なった結果からして，*Anomalops* の発光体は発光バクテリアではないと考えた。Bassot (1968) は *Anomalops* の固定標本の組織を調べて，発光バクテリア説を支持した。

私等はこの点を明かにするため，充分な材料にて，羽根田はバンダ島滞在中，次のことを実験し，辻は発光器の乾燥材料について，アデノシン三燐酸，その他数種の Cofactor に対する反応を調べ，発光細菌か否かをきめる材料とした。

発光器内容の懸濁液の観察

Anomalops および *Photobrepharon* の発光器を滅菌海水および真水にて emulsion とし，暗所にて発光の有無を観察した。海水 Emulsion では，これを低温に保てば 10 時間後もなお発光を認めたが，真水では光は直ちに消光した。

海水 Emulsion を静置すると空気にふれる表面 2～3 mm は発光するか深部は消光する。これを，ふると全液が発光するが，静置するとまた表層のみ発光，深部は消光する。

この Emulsion の光は温度により変化し，23～26°C が最も光は強く，50°C で消光，5 分以上 50°C に保つと，冷却しても，光を快復しない。発光器を完全に乾燥した後，水を加えても発光しない。

発光器の冷水，及び熱水浸出液を作り，両者を暗所で混合したが発光を認めなかった。

発光体 Emulsion に adenosine 5′-monophosphate, adenosine 5′-diphosphate, adenosine 5′-triphosphate, reduced nicotinamide adenine dinucleotide, reduced nicotinamide adenine dinucleotide phoshate および Coenzyme A をそれぞれ加えたが陰性であった。

しかし，乾燥発光器の細胞を除いた浸出液を作り，遠心沈澱後，上澄液に FMN (Flavin mononucleotide) に n-dodecyl aldehyde を加えたとき発光を認めたことは，浸出液にバクテリアのルシフェラーゼの存在する証明となるものである。

発光器よりの発光バクテリア培養試験は法のように行ない，培養基として，3% 食塩加普通寒天，3% 食塩加イカ汁寒天を用いた。

培養試験の結果はすべて陰性であった。発光器の海水 10% Formlin 標本についての電子顕微鏡切片，製作，写真撮影は日本電子株式会社の好意でなされた。Fig. 3, 4 はそれぞれの発光器の 17,000 倍の写真である。

以上の実験，培養結果，電子顕微鏡像よりみると，両種の発光体内容は化学物質ではなく魚と共生する発光バクテリアであると考えられる。多くの共生発光による発光魚，マツカサウオ *Monocentris japonicus*, オーストラリアのマツカサウオ *Cleidopus gloria maris*, チゴダラ *Physiculus japonicus*, トージン *Coelorhynchus japonicus* ハリダシエビス *Paratrachichthys prosthemius* ホタルジャコ *Acropoma japonicum*, *A. hanedai* ヒイラギ *Leiognathus equnlus, Gazza minuta* の共生発光バクテリアが，ほとんどどんな培養基にも容易に培養できることを考えると，本魚2種は何故，培養できないか，このことにつき，電子顕微鏡像をみると，Bush & Chapman (1961) がアメリカのゴキブリ *Periplaneta americana* より得た bacteroids と形態がにている。bacteroids は原始的なバクテリアの一群と考えられ，未だ培養に成功していない。

本魚の Emulsion の反応が Bacteria であり，培養できない点，電子顕微鏡像の形態からして，本魚の発光体は魚と共生する一つの新しい発光する Bacteroids か，それに近い種類ではなかろうか。

Although bioluminescence is a very common characteristic of deepwater fishes, some shallow-water fishes are also known for their luminosity. Among the most famous are those belonging to the small family Anomalopidae, which consists of three genera and species: *Anomalops katoptron*, *Photoblepharon palpebratus*, and *Kryptophanaron alfredi*. *Kryptaphanaron* is known from a single specimen caught at Jamaica, West Indies, by Dahlgren (1908) and described by Silvester and Fowler (1926). *Anomalops* and *Photoblepharon*, the best known members, are indigenous to the waters around the Banda Islands, located at the eastern end of the Indonesian Archipelago. When observed at night, *Anomalops* produces a series of rapid flashes as it swims through the water. The light from *Photoblepharon* is more nearly continuous and flashing is infrequent. The blinking produced by the fishes is so spectacular that they have drawn the attention of students of bioluminescence over the years. However, due to the remoteness of the region in which these fishes occur, relatively few studies have been carried out.

The studies by Vorderman (1900), Steche (1907, 1909), Harvey (1921, 1922, 1925), Haneda (1943, 1953, 1955), and Bassot (1968) have shown that the light is emitted from a pair of relatively large flat structures, roughly elliptical in shape, each lying in a suborbital depression. The light-emitting face of the organ is cream-colored, whereas the opposite face is nearly black due to a black pigmented cell layer. The lightemission is continuous. The gross anatomy and histology of the light organs in the two species are also very similar. Each organ is filled by many parallel tubes that run from the pigmented base layer to the transparent, cream-colored face. Numerous blood capillaries also run parallel to the tubes. When a transverse section across the tubes is examined, the tubes are found to have a polygonal shape and are arranged in a rosette pattern around the capillaries. The tubes contain what appear to be bacteria, which, if luminous, could account for the constant light emitted by the organ. The methods employed by each fish to extinguish its light are unusual. In *Anomalops*, this is accomplished by rotating the entire organ along its long axis so that the luminous face is turned down and toward the body, presenting the pigmented face to the outside. The rotation takes place through a small cartilagenous tissue located at the dorsoanterior edge which attaches the light organ to the fish. In the case of *Photoblepharon*, however, the light is extinguished by drawing up a black fold over the organ. Why two species so closely related and with organs so similar anatomically should develop entirely different methods for occuluding the light remains a mystery.

Most previous studies have indicated that symbiotic luminous bacteria present in the tubules are responsible for the light production. Thus, Harvey (1922) found that an emulsion of a light organ in sea water behaved similarly to an emulsion of luminous bacteria. Bassot (1968) has found stained sections of the light organs of *Anomalops* to contain bacteria in the tubules when examined with a light microscope. However, Harvey (1922) and Haneda (1943) could not obtain a culture of luminous bacteria from the organs. This finding is potentially significant since virtually all symbiotic luminous bacteria obtained from the light organs of fish, for example, *Leiognathus, Physiculus, Monocentris,* and *Acropoma,* are culturable on synthetic agar medium. The present study, threfore, was undertaken to investigate this problem further.

Materials and Methods

Photoblepharon and *Anomalops* were collected a short distance offshore at Banda Islands, Indonesia. Collection was carried out at night from a boat, using hand nets in waters 4–5 meters deep. The fishes were easily located because of their intermittent flashing as they swam through the clear water. Moonlight appeared to cause them either to lessen their flashing or to hide among the corals and rocks, whereas they were more evident in numbers during periods of darkness, such as when the moon had set.

Living specimens were placed in a large glass jar containing sea water and studied in the dark. Other specimens were used immediately for chemical and bacteriological experiments. For preparing luminous emulsions of the light organ, 4 fresh organs were gound in approximately 5 ml. of sea water using an all-glass homogenizer. In the chemical tests, a few milligrams of cofactor were dissolved in a few ml. of sea water and the solution was then added immediately to the emulsion. Bacteriological studies were performed with two different culture media. The first consisted of a squid juice-agar medium containing in 1 liter of water, 30 gm. NaCl, 5 gm. peptone, 1 ml. glycerol, 15 gm. agar, and squid juice extract, with pH adjusted to 7.2–7.4. The second consisted of a nutrient agar medium containing in 1 liter of water, 30 gm. NaCl and 23 gm. nutrient agar, with pH adjusted to 6.8.

Some specimens were preserved for later studies. For the electron microscopic work, the detached photophores were placed in 10% formalin sea water. After about 2 months, the photophores were washed with distilled water and fixed in 1% osmium tetroxide for 1.2–2.0 hrs. The tissues were then dehydrated through a graded series of acetone as follows: 30, 40, 50, 60, 70, 80, 85, 90, 95, and 100%. Embedding was in eooxyin A and B (A:B=5:5). Ultrathin sections were cut with a JUM-type 5B microtome. Sections were then examined in a JEM-type 7A electron microscope. For the bacterial luciferase test, air-dried photophores were used.

Results

1. *General observations.* Fig. 1 shows the photographs of *Photoblepharon* and *Anomalops*. The light organs are prominently displayed beneath the eyes. In a specimen of *Anomalops* 94 mm. in standard length and 32 mm. in depth of body, the light organ measured 11 mm. in the long axis, 4 mm. in the short axis, and 1 mm. in thickness. In a specimen of *Photoblepharon* 80 mm. in standard length and 30 mm. in depth of body, the corresponding measurements were 9.1 mm. × 5.6 mm. × 1.0 mm. Viewed laterally, the body of *Photoblepharon* had a rounded appearance, whereas the body of *Anomalops* was elongate.

The natives of Banda call *Photoblepharon*, "ikan laweri batu, or the "fish that lives among the rocks, ' and *Anomalops*, "ikan laweri air, ' or the "fish that lives near the surface." In reality, both species lived among the lava rocks and coral, and came out mostly at night. *Anomalops* swam in schools of 20–50 near the surface, blinking rapidly as they swam. *Photoblepharon* behaved differently. They swam either singly or in pairs, darting in and out from among the rocks and corals. They came to the surface only occasionally. They extinguished their light only infrequently and thus the light shone almost continuously with constant intensity.

Observations were also carried out on *Photoblepharon* and *Anomalops* held individually in

large glass jars. When placed in a semi-darkened room, both displayed their luminous organs continously and the light intensity appeared to be constant. When *Anomalops* was moved to a lighted room, the light organ was rotated to a darkened position almost immediately. The angle through which the organ was rotated was 120–135° in a downward direction. The light-emitting surface moved out of view, thus cutting off the light. When *Photoblepharon* was moved from a semi-darkened to a lighted room, the fish did not occulude its light most of the time. When both fish were returned to the semi-darkened room, *Anomalops* displayed its light immediately, whereas *Photoblepharon* showed little change in luminescence behavior. When a flashlight beam directed at them was turned on-and-off, they responded in the same manner as to constant light. Physical handling of the fishes did not seem to affect either their blinking or light intensity.

2. *Chemical studies.* The luminous emulsions prepared from the light organs quickly became dark when allowed to stand, except for a layer at the top 2–3 mm. thick. When the darkened emulsion was shaken in air, the luminescence was completely restored. Standing produced the same result. Such an emulsion retained its ability to luminesce for many hours, perhaps 6–8 hrs.

Raising the temperature slowly caused a gradual decrease in light intensity until at around 50°C, the emulsion became completely dark. Lowering the temperature to around 26°C did not restore the luminescence. Light intensity appeared to be optimal between 23–26°C.

When an emulsion was diluted with fresh water, luminescence was quickly extinguished. Diluting with sea water decreased the light intensity, but only in proportion to the volume of sea water added. When a luminous organ was ground in fresh water, the light was also immediately extinguished. Air-dried organs did not luminesce when moistened with water.

Tests for the presence of the luciferase-luciferin (enzyme-substrate) reaction in the organs were also performed, using cold- and hot-water extracts. The cold-water extract (luciferase) was prepared by grinding 4 fresh organs in about 5 ml. of water. The hot-water extract (luciferin) was prepared by grinding 4 fresh organs for 1 min. in about 5 ml. of boilding water and immediately cooling in cold water. The two extracts, when mixed, gave no light, indicating the absence of the luciferase-luciferin reaction.

Attempts were also made to stimulate light emission from dark, cold-water extracts by mixing cofactors known to stimulate extracts of other luminous organisms. The following cofactors were added with negative results: adenosine 5′-monophosphate, adenosine 5′-diphosphate, adenosine 5′-triphosphate, reduced nicotinamide adenine dinucleotide, reduced nicotinamide adenine dinucleotide phosphate, and coenzyme A.

The most successful results were obtained with cell-free extracts of air-dried organs. The extracts were prepared by homogenizing 2 air-dried organs in 5.5 ml. of distilled water. After centrifuging at 10,00×g for 10 min. at 2°C, 2.5 ml. of the supernatant were mixed with 1.0 ml of a dilute solution of reduced flavin mononucleotide (FMN) plus a trace amount of n-dodecyl aldehyde. Light was recorded for all samples of cell-free extracts tested, indicating the presence of bacterial luciferase in the extracts.

3. *Bacterial culture studies.* Using media previously described, numerous attempts were made to culture luminous bacteria from the light organs. The results were completely negative and, occasionally, when some growth was obtained, luminescence could not be detected.

4. *Electron microscopy.* Electron micrographs of the light organs of both species are shown

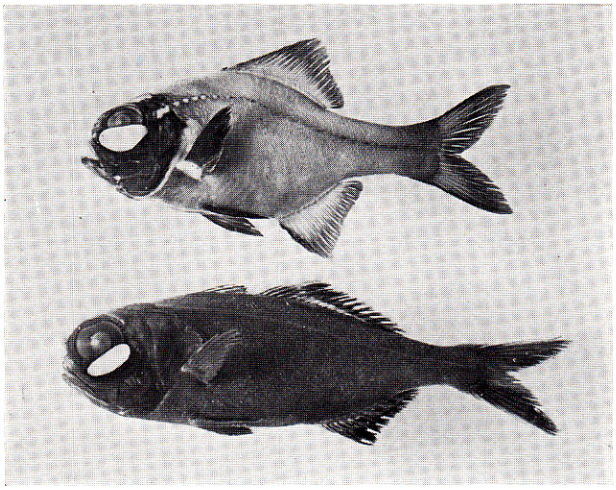

Fig. 1. *Photobrepharon palpebratus* (above) と *Anomalops katoptron* (below)

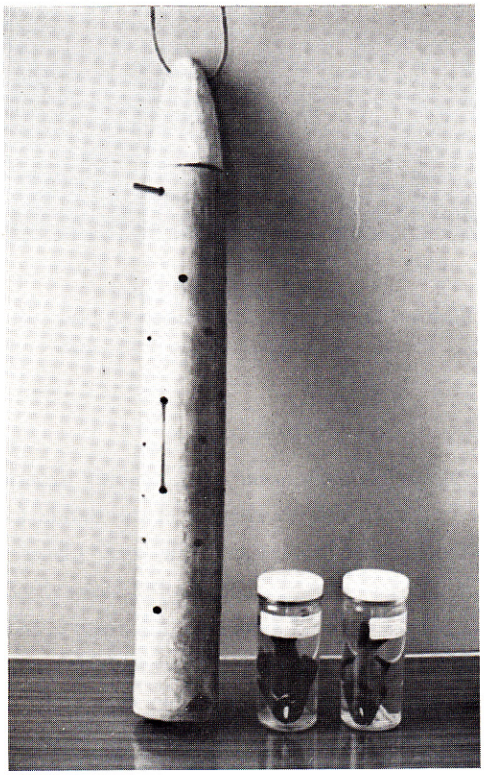

Fig. 2. バンダの2種の発光魚の標本と発光魚の飼育器ブブ (Bubu)
バンダの漁夫はこの竹の飼育器に生きた魚を入れて釣に出かける.
Bubu, bamboo tool of *Anomalop* and *Photobrepharon* for fishing and the specimens.

in Figs. 3 and 4. They represent magnifications of ultrathin sections of the light organs, prepared as previously described. Both photographs show large numbers of bacterial particles in varying dimensions. Such particles were observed in all sections taken through the middle of ihe organ. The large, rod-like particles are about 2.4 microns in length and 0.92 microns in diameter.

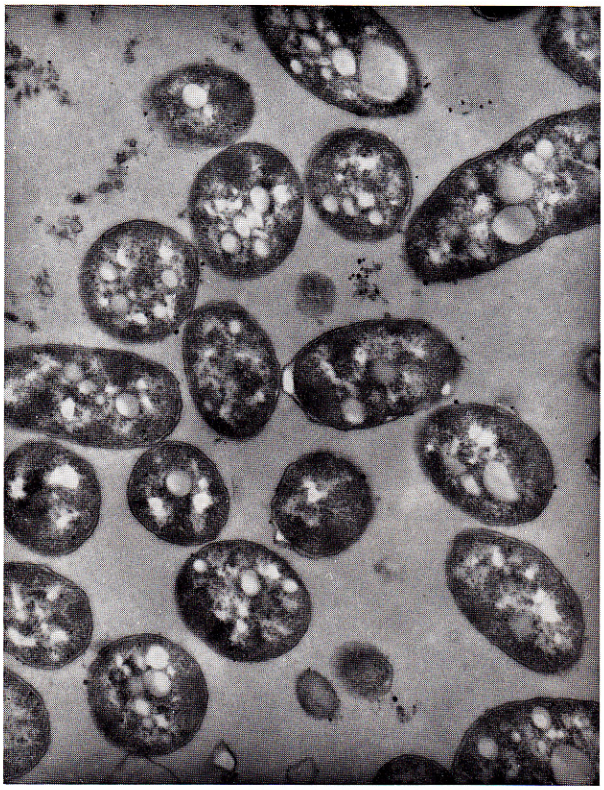

Fig. 3. フォトブレファーロンの発光体
電子顕微鏡像. ×17,000
Electron micrograph of the luminous body of
Photobrepharon palpebratus ×17,000.

Discussion

According to Harvey (1952), *Photoblepharon* is found only around Amboina and the Banda Islands, whereas *Anomalops* is known more widely from the Banda Islands westward to the New Hebrides and Fiji Islands. Reports of *Anomalops* in the latter places, however, have been scarce. Haneda (1952) has also reported observing large schools of blinking *Anomalops* at night on the northwest coast of West Irian. Eight specimens of *Anomalops* have also been reported from Japan by Abe (1942, 1951) by Haneda (1955) and Kamohara (1961), but none recently. From all accounts, both *Photoblepharon* and *Anomalops* appear to be uncommon except in regions close to Banda. The difficulty of obtaining specimens, threfore, has contributed to the limited number of studies that have been carried out and to the lack of information on their methods of light production.

The results obtained in the present study, taken together with those obtained by earlier workers, however, show conclusively that the luminescence in *Photoblepharon* and *Anomalops* is due to symbiotic luminous bacteria. The results of this tudy which support this conclusion may be summarized as follows: dependence of the luminescence on oxygen concentration; extinction temperature for the luminescence of around 50°C; extinction of the luminescence of an emulsion on dilution with fresh water; non-luminosity of dessicated organs on moistening with water; and negative luciferase-luciferin reac-

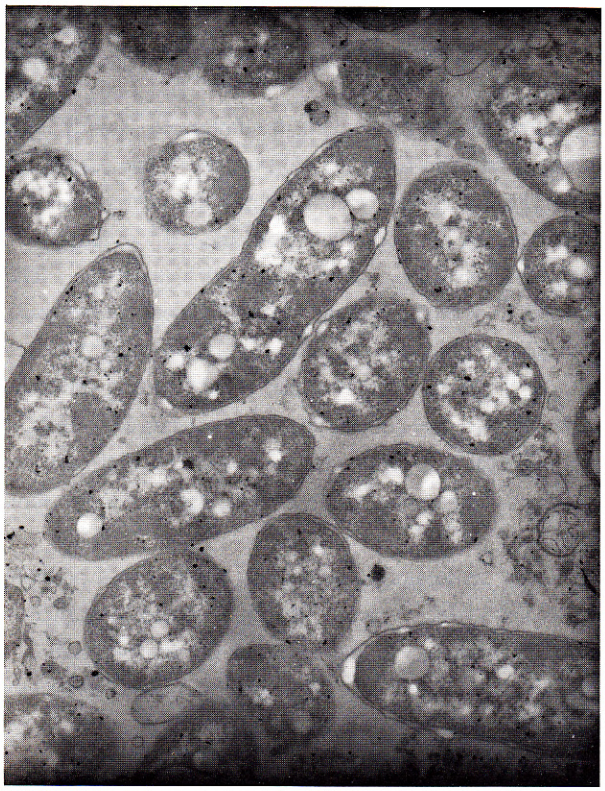

Fig. 4. ヒカリキンメダイ *Anomalops* の発光体
電子顕微鏡. ×17,000
Electron micrograph of the luminous boody of *Anomalops katoptron*. ×17,000

tion. Almost the same results were obtained by Harvey (1922), who concluded that the luminescence is due to symbiotic luminous bacteria because of the similarities in the chemical behavior of sea water emulsions of the organs with that of sea water suspensions of luminous bacteria. Harvey (1922) also advanced other evidence: the effect of cytolytic agents and sodium fluoride in diminishing the luminescence of an emulsion, the sensitivity of the luminescence to potassium cyanide, and the presence of numerous rod-shaped bacteria in smears of the organs. The fact that the light organs contained many tube-like structures, supplied with a rich blood supply, suggested to Harvey (1922) that these organs were especially constructed to provide nourishment and oxygen to bacteria. Symbiotic luminous bacteria normally require large amounts of oxygen.

Bassot (1968) has also reported finding spherical or rod-like bacteria, always less than 2 microns in length, in stained organ sections of *Anomalops*. The electron micrographs obtained in this study, which indicate the presence of rod-like bacteria with dimensions approximating 2.4 microns×0.92 microns, confirm the latter findings. The light organ of *Photoblepharon* also appears to contain similar bacteria.

The most convincing evidence, however, comes from studies with cell-free extracts of the organs. When a dilute solution of reduced FMN is injected into extracts containing a trace of n-dodecyl aldehyde, light is emitted. Since bacterial luminescence is due to a reaction involving oxygen, bac-

terial luciferase, a long-chain aldehyde, and reduced FMN, the finding indicates that bacterial luciferase is present in the extracts. It is reasonable to conclude that the organs, therefore, contain symbiotic luminous bacteria.

The purpose of this study has been to explain the failure of Harvey (1922) and Haneda (1943) to obtain cultures of luminous bacteria from the light organs. The reason still remains unclear and must await future study. The failure to obtain bacterial cultures is indeed very surprising in view of the ease with which cultures may be obtained from the light organs of *Monocentris, Cleidopus, Physiculus, Coelorhynchus, Paratrachichthys, Acropoma,* and *Leiognathus.* The reason may be in the condition of the medium, such as in the lack of an essential nutrient, as previously suggested by Harvey (1922). However, the morphology of these organisms appears to resemble the morphology of certain bacterioids as observed under the electron microscope, as for example, the bacteroids studied by Bush and Chapman (1961) in the developing oocytes of the American cockroach, *Periplaneta americana.* Such bacteroids are considered to be primitive forms of bacteria and have not been cultured. The luminescence of *Photoblepharon* and *Anomalops*, therefore, may be due to luminous bacteroids or to organisms similar to them.

As in the case with nearly all luminous organisms, the function of bioluminescence in *Photoblepharon* and *Anomalops* is unknown. Possibly, the light is used to attract prey or even to see. It is interesting to note that the fishermen of Banda, as in the time of Harvey's (1922) visit some 50 years ago, still use the light organ as a lure. The organ is cut of the fish and is attached to the line about 10 cm. above the baited hook. The organ remains luminous for many hours and is said to attract fish.

Summary

The methods of light production in *Photoblepharon* and *Anomalops* have been investigated, using fresh and preserved material. Based on biochemical evidence obtained from emulsions of the organs and on cell-free extracts, especially the stimulation of luminescence with reduced FMN, and on electron microscopy of organ sections showing the presence of numerous bacteria, it is concluded that the light is produced by symbiotic luminous bacteria. However, the morphology of these luminous bacteria appears to resemble the morphology of certain bacteroids. The luminescence of *Photobrepharon* and *Anomalops* may due to luminous bacteroids or to organisms similar to them.

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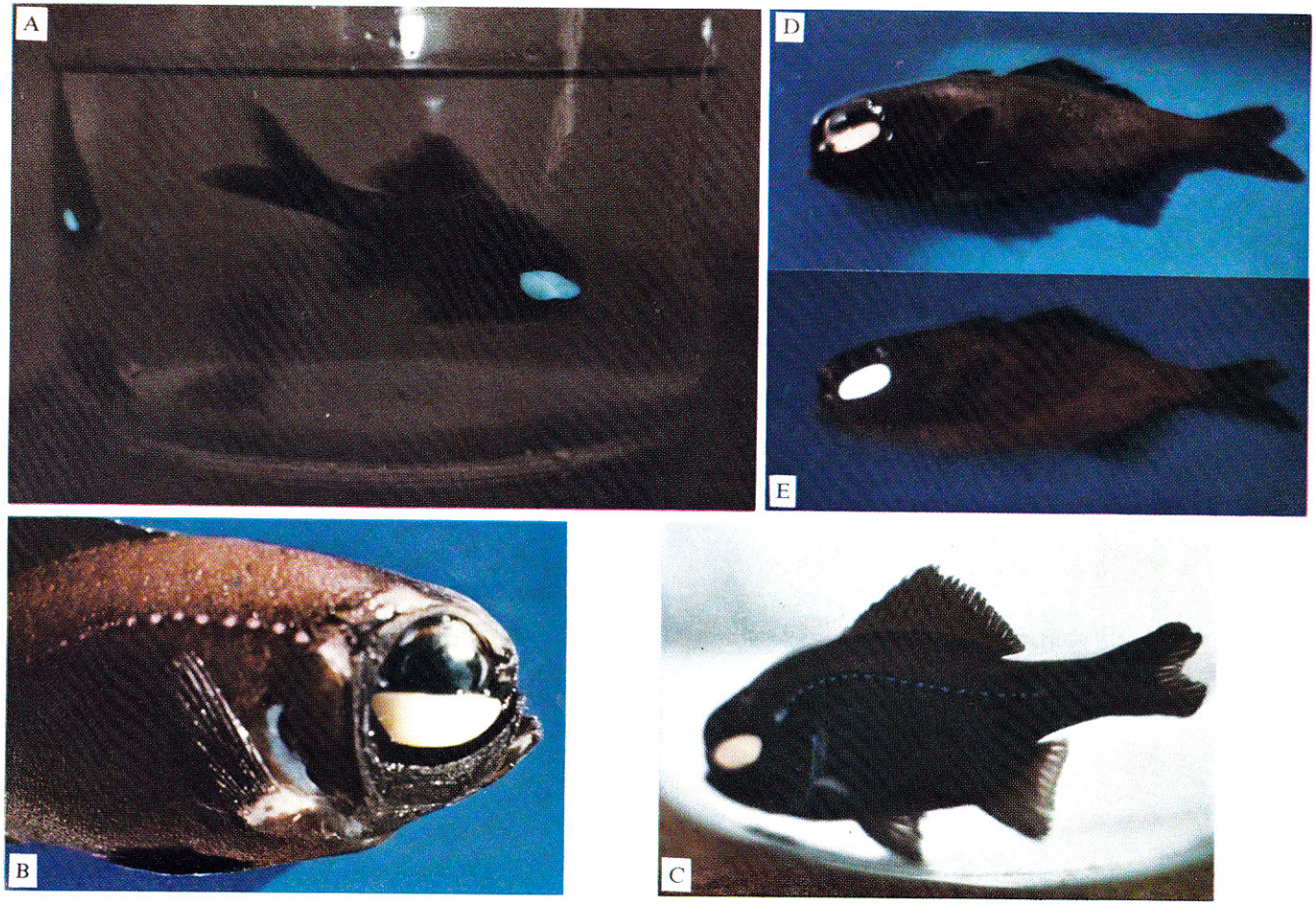

バンダ島の2種の発光魚フォトブレファーロン *Photobrepharon palpebratus* (A, B, C) とヒカリキンメダイ *Anomalops katoptron* (D. 室内光で撮影. E. 魚の光で撮影)