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発光性頭足類の研究

ツメイカ科 (*Onychoteuthidae*)

岡　田　　要*

Study of Luminous Cephalopoda II
Light Organs of *Onychoteuthis*

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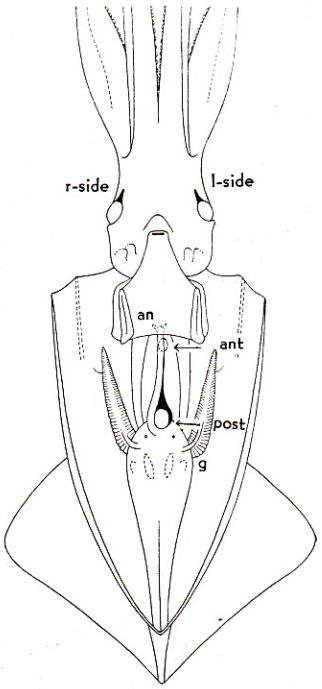
(With 1 Plate)

6属約 20 種といえば，開眼イカ類の中では科として決して小さな群とはいえないが，その中で「発光能力あり」と断言できるのは外套腔内に発光器を有するツメイカ属 (*Onychoteuthis*) だけである。CHUM, C. (1910) は *Chaunoteuthis mollis* の外套腹面の皮膚に発光器の存在を指摘しているが，これは G. PFEFFER (1912) によって否定されている。

ツメイカ属は種類こそ少ないが，世界の各水域に分布して，大西洋でも地中海でも，また太平洋でも各所で捕獲されており，すでに 19 世紀の初め W. E. LEACH (1817) によって *Loligo banksii* の名で記載されている。現行の属名 *Onychoteuthis* は後に K. M. H. LICHTENSTEIN (1818) によって提唱されたものである。

ツメイカ類はこのように分布が広いだけに地理的な変異もあり，相次ぐ新種の発表も少なくはなかったのであるが，1912年 G. PFEFFER の再検ですべて *banksii* の種名の下に統一されてしまった。にも拘らず著者 (1927) は先輩佐々木望氏 (1916) がすでに *banksii* として記載した本邦北海道産の標本に対して，外套その他の部分の長さの測定と発光器にみる構造上の相違から大胆にも新種の設立を試みたのであった。それが以下に記す日本北ツメイカ，*Onychoteuthis borealijaponica* であって，原記載 (OKADA, 1927, p. 5) に語尾が *borealijaponicus* となっているのは文法的誤りである。ツメイカの発光器は米国のイカ学者 W. E. HOYLE (1909) によって外套腔内に発見された内臓器官 (visceral organs) であって，鰓より前の内臓腹面の中央線上に前後にならぶ2個の単独器官からなっている (第1図)。後方の墨汁嚢上にあるものは (以下後方器官と呼ぶ) ほぼ球形で，大豆粒の大きさを有し (長径5 mm)，直腸基部の左側 (図では向って右側) に偏してなか



第1図　ツメイカ *Onychoteuthis* の外套を腹面中正で切開して腔内に発達する発光器を示す

The mantle of *Onychoteuthis* is longitudinally cut open on ventral side, to show the location of photogenic organs, *ant*, anterior organ; *post*, posterior organ; *l*-side, left side; *r*-side, right side.

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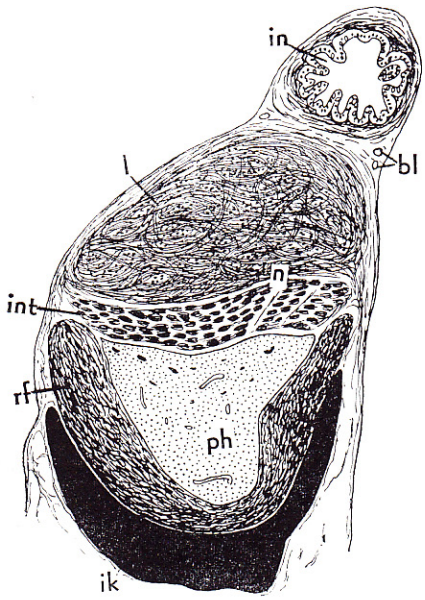
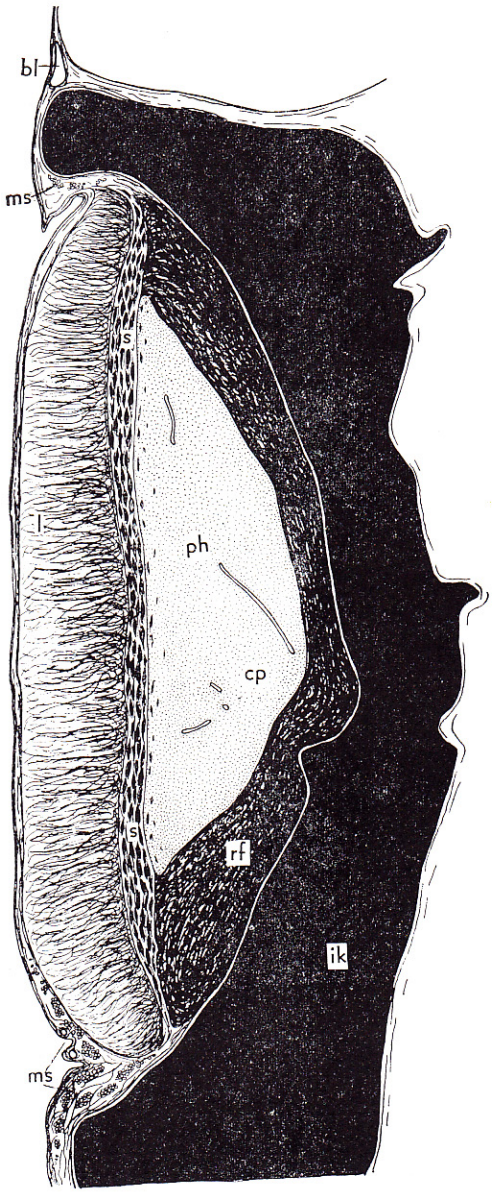
ば墨汁嚢内に没している。これに比べて前方器官ははるかに小さく（長径 3 mm 半），位置が肛門に近く墨汁排出管上にある関係から墨汁による色素環の形成は後方器官ほど発達していない。またこの器官の特徴は前面が直腸の末端部でおおわれていることである。

Naef, A. (1923) はこれら 2 つの内臓器官の外に眼球の腹面にある黄色の枕状の隆起を発光器として挙げている（96頁の引用文参照）。いかにも頭足類の眼球腹面は彼の指摘するように発光器の発生場所としてはきわめて出現頻度の高いものであるが，著者のみた限りではどうもこの Naef の提案には賛成しかねる。それに比べて上記 2 つの内臓器官は構造の上からも発光器官として疑う余地はない。ところで Naef は外套の背長わずかに 11 mm のごく若い *banksii* 幼生では，前方器官の位置も後方器官と同様直腸の右側であって，前記のように直腸の末端部でおおわれるようになるのは後になっておこる二次的変化であるといっている。日本キタツメイカ *borealijaponica* では外套の背長 220–243 mm にも達し，この種のイカとしてはすこぶる大きなもので，おそらく充分に成育していると思われるにも拘らず，前方器官の位置が依然として直腸の右側である。そして内部の構造が後述するように前後両器官とも *banksii* のものと比較して明瞭に相違している。そこで著者はこれらの事実を理由に，このイカに対して新種の設立



第 2 図　バンクシ・ツメイカの前発光器の横断
Transverse section of the anterior phogenic Organ of *Onychoteuthis banksii*, ×24

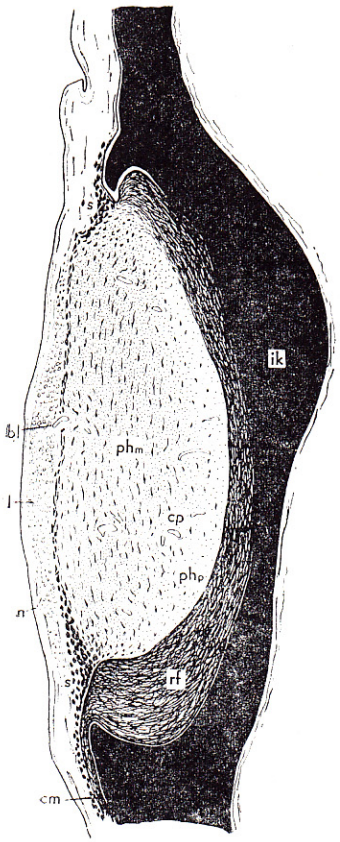


第 3 図　バンクシ・ツメイカの後発光器の縦断
Longitudinal section of the posterior organ of the Same species, ×24

を提案したのであったが，佐々木氏 (1929, p. 230) はその受入れを拒否した。

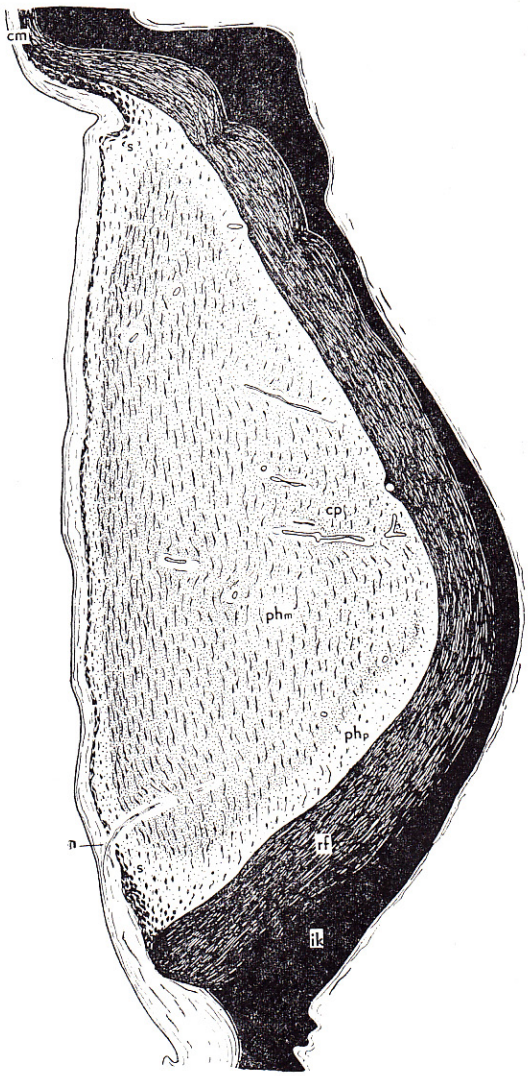
"To my regret I am not able to offer here any definite opinion upon his view as no specimen from other countries in represented in the collections at my disposal," と一応は確答を避けてはいるものの "but it should not be forgotten that the development of luminous organs sometimes differs with age as well as with the season of the year, and it seems to be risky to determine the specific relationships merely by the structure of the luminous organs of a small number of specimens." と最後は明らかに反対の態度を示している。

ツメイカの発光器は球形の比較的底のあさい楕円状の窩の中に積み重ねられた3乃至4層からなり，各層の構造は種内では前後両器官ともほぼ等しいが，異種間ではかなりの相違が認められる。そこで先ず *banksii* の後方器官を例としてその概略を述べると，第3図にみるとおりほとんど中心部に近く，よく発達した発光組織の大きな塊 (median photogenic tissue



第4図　北日本ツメイカの前発光器の縦断

Median longitudinal section of the anterior photogenic organ of *Onychoteuthis borealijaponica*, ×18



第5図　北日本ツメイカの後発光器の縦断

Similar section of the posterior Organ of the same sepcies, ×18

after Hoyle) があり，これを取巻いて後方では繩の如くによじれた有色（赤褐）の繊維層よりなる反射層 (*rf*)，また前方では Hoyle によって中間層 (intermediate layer) とよばれた菱形鱗片層 (*s*) とその外側をおおう可なり部厚なレンズ層 (*l*) が見られる。ただしレンズ層を構成する繊維は中間層や反射層を構成するものとは異なり，だいたいが発光面に直角の方向に配列されていて，ヘマトキシリン染剤に対して着色しない。ところで同種内の前後両器官の構造は第2図と第3図，または第4図と第5図の比較でも容易に認められるように相違はごくわずかで，大体が各層の厚さの比率の差であるとか，後部にある墨汁嚢との関係のちがい程度のものであるが，異種間での相違はきわめて顕著で，ことに中央の発光組織と前方のレンズ層の構成は根本的に異なっている。たとえば北日本ツメイカでは前後両発光器とも中間層の発達がきわめて悪く，極度に薄化してわずかに内部の発光組織を外側の真皮層から区画する程度のものにすぎない。そして元来中間層として発達すべき筈の菱形鱗片 (*s*) は表面の 1～2 層だけを残して他はすべて解体して発光組織のほとんど全域に拡散している（図版参照)。しかもこの事に関連してか日本北ツメイカの発光組織はヘマトキシリン染色に対して周辺部は脱色しても，鱗片を含む中心部はなかなか脱色せず，つねに青色が残る（第5図参照)。それともこれは発光組織にありがちな，そこに含まれた特殊顆粒の存在によるものであろうか。いずれにせよツメイカの発光組織 (*ph*) は種類，器官をとわず緊密なシンシチュームで核は明瞭にみとめられるが細胞の区分はまったくみられない。ただし組織間には自由に走る毛管系の発達があり，また神経も外側の真皮層から入りこんで来ている。なお前方肛門に近い位置にある発光器も，それが同一の北日本ツメイカである限り構造はほぼ上述の通りであるが，この発光器には中間層の外側にごく程度の低いレンズ層 (*l*) の発生の兆がみられる。

最後にツメイカ類の発光器には *banksii*, *borealijaponica* のいずれにも光の後方透入をふせぐための色素層の発達がない。ただしこれは発光器の占める位置からして墨汁嚢，あるいはその派生によって代行されているからである。なお北日本ツメイカにおいては前発光器と後発光器はたがいに相対する端で反射層と同質の繊維の帯 (*c*) で連結されている（第 4，第 5 図)。このことからツメイカの2つの発光器は前報告で紹介したトリイカ (*Ornithoteuthis volatilis*) の線状の内臓発光器と同じ成因のものかとも思われるが，*banksii* ではこのような連結帯はなく，各発光器官はそれぞれ独立して一方は肛門器 (anal organ)，他方は墨汁嚢器 (inksac organ) をなしている。

This kind of squids seems not rare in the Atlantic and Mediterranean Seas, and it is distributed widely also in the Pacific Ocean. *Onychoteuthis banksii* was first described by W.E. Leach (1817) as early as the beginning of the last century under the name of *Loligo banksii*, but photogenic organs were detected in the mantle cavity ninety years later by W. E. Hoyle (1909).

In the latest monograph on the Mediterranean Cephalopods, A. Naef (1923, p. 320) pointed out that "ausser diesen, schon Hoyle bekannten Leuchtorganen der Mantelhöhle, stehen zwei mächtige gelbbraune, kissenartige Organe auf der Ventralseite des Augenbulbus, medialwärts vor und unter den Fenstern", and suggested that "es können nach Form und Lage nur Leuchtorgane sei." The surface of the ventral hemisphere of the cephalopodian eye-ball is indeed the region where the organs of this nature occur most frequently, but in this case at least their photogenic ability is quite doubtful. On the other hand, when the mantle cavity of this squid is opened, one's attention is at once attracted by a round body of about bean size lying in the middle of the visceral mass (Fig. 1). The posterior organ is located in a hemispherical depression of the ink-sac and the commencement of the rectum forms a semicircular loop on its right side, while the anterior organ is found on the median axis of the visceral mass and the rectum passes over it. In the Japanese specimen, however, the anterior organ is not covered by the rectum, but the latter passes by its right side as in the posterior organ. Moreover, the anterior and posterior organs are connected by a median longitudinal commissure.

According to Naef (l.c.), in a young specimen, 11 mm in dorsal length of the mantle, of *Onychoteuthis banksii* the anterior organ is found on the *right*[1] side of the rectum immediately below the anal papilla and its position becomes axial afterwards. If this is corect, the right-sided situation of the anterior organ in the Japanese species may indicate a primitive type of arrangement, from which the axial situation of the corresponding organ of *banksii* might have been derived. However, the Japanese species is larger than the average size of *banksii*, and histological structure of the light organs is quite different. For these reasons the writer proposed in 1927 a new name *borealijaponica* for the Japanese species to distinguish it from the known Onychoteuthid.

To this proposal Sasaki (1929, p. 230) stated "to my regret I am not able to offer here any definite opinion upon his view as no specimen from other countries is represented in the collections at my disposal. But it should not be forgotten that the development of luminous organs sometimes differs with age as well as with the season of the year and it seems to be risky to determine the specific relationships merely by the structure of the luminous organs of a small number of specimens," apparently setting himself against the new name.

The photogenic organs of *Onychoteuthis* (Figs. 2–5) show distinctly three or four-fold differentiations of more or less parallel layers formed in a limited region and arranged on a

1) The original paper writes *left* side, which means that when the mantle is cut open the anterior organ is found on the left as viewed from the observer. It is actually on the right side of the squid body, as shown in Fig. 1.

proximodistal axis. The mode of differentiation of the layers is practically the same in both anterior and posterior organs within the species but differs in different species. The photogenic organ of *banksii* (Figs. 2–3) consists of 1) median photogenic tissue, 2) reflector, 3) the so-called intermediate layer of Hoyle and 4) lens, while the same organ of the Japanese species (Figs. 4–5) is almost without lens and the intermediate layer is poorly developed. But the most striking distinction between the two species appears in the central mass of the photogenic tissue which is, in either case, syncytial without cellular boundaries. After the ordinary procedure of staining with dyes such as iron haematoxylin we find in the tissue of the Japanese species a large number of scaly lamellae with a particularly dark blue colour (pl.–figs. S).

Hoyle 1909 did not mention the presence of such lamellae in the photogenic tissue of his specimen of *Onychoteuthis*. In fact the structure could not be found in the photogenic tissue of the Pacific *Onychoteuthis* obtained from more southern parts of Japan (Fig. 2, 3). In either case, however, the light organs in the preserved condition are seen as dull white round bodies surrounded by a black ring. The pigment layer as usual in these organs in the mantle cavity, is due to the pigment of the ink-sac which forms a hemispheric depression in which they are located. The pigment naturally functions as a blind to shut up the inward penetration of light. Therefore no special pigment sheath is necessary to occur in this case.

Inside the pigment comes a thick layer of parallel fibres (*rf*) which assume from the first a reddish brown tinge as if they have been stained by the pigment of subjacent ink-sac. The layer is as a whole concave against the outer luminous center and convex toward the posterior ink-sac. It constitutes a parabolic mirror to which the term reflector is applied. The layer is nearly uniformly thick, about 7 mm in *banksii* and 14 mm in *borealijaponica*, but strictly speaking the thickness differs in parts, in the anterior organ of the latter at least thickest is near the inferior end, gradually thinning towards the opposite end. In the Japanese species moreover the fibres of the reflector extend into the median longitudinal commissure that connect the anterior organ to the posterior (Figs. 4, 5 *c*).

The tissue filling up the concavity of the parabolic mirror-like reflector is syncytial. There are no visible cellular structures except nuclei, but this part receives a rich supply of bolod capillaries, and a preparation stained with iron haematoxylin is blue perhaps due to impregnation of fine granules, although the presumed granules are so small that they are almost invisible under the light microscope even with a high power magnification.

As stated already, the central syncytium of *borealijaponica* contains a large number of scaly lamellae (Figs. 4, 5 *s*). They are placed parallel to one another in layers. Their functions are doubtful but can be comparable to the 'central scales' in the middle part of the luminous organs of *Pterygioteuthis* and *Pyroteuthis* (Hoyle 1902, '04), or to the 'tige cristalline' of the *Abralia*n photophores (Joubin 1895). In any case the lamellae in question occur everywhere throughout the photogenic tissue, being particularly abundant near the outer surface. In *banksii* there are no such scaly lamellae in the central tissue but they appear outside the tissue in a distinct layer which Hoyle named the intermediate layer (Figs. 2, 3 *int*). It has a thickness

of more than 6 mm and is made up of several layers of regular fusiform scales arranged with their longer axis parallel to that of the organ.

The integument in front of the anterior organ of *borealijaponica* is slightly thickened and its texture is somewhat modified (Fig. 4 *l*), but since this part is almost indistinguishable from the ordinary integument that covers the visceral mass as whole, it is open to question whether this slightly modified integument may deserve to be described as a lens. Such a lenticular thickening is entirely absent in the posterior organ (Fig. 5). In *banksii*, however, the front of the photogenic organ presents another view. Here the lens attains a considerable development, about 30 mm in thickness (Figs. 2, 3 *l*). It rests upon the outer margin of the reflector and has a plano-convex shape, the convex surface being directed outwards. Its thickness is made up of delicate fibres having a more or less wavy course from inner side to outer side.

While the scales of the intermediate layer, the scaly lamellae of the central synstium, and the fibres of the reflector are stained deep blue with haematoxylin, the fibres of the lens only take the counter stains such as eosin and orange G. The fact suggests that the lens is made up of fibres of different nature, perhaps same as that of the integument. Blood vessels pass almost virtically throughout the thickness of the lens and intermediate layer from outer to inner, and brach out into capillaries in the central photogenic tissue which receives also branches of the nerve (Figs. 2, 4, 5 *bl*, *nv*). The origin of the latter has not been traced, but probably it comes from the visceral ganglion as a branch or branches of the ink-sac nerve.

Although no actual observation of the light production in this squid has been made yet, it is almost certain that the organs with such structure as described are photogenic as they are well designed for this function. To the primary tissue with its invariably abundant blood and nerve supply, are added an efficiently developed reflactor, a pigment cup (formed by the lateral expansion of the ink-sac) and a lens. Moreover, existence of photogenic organs in the mantle cavity is not rare among cephalopods (for example, *Chiroteuthis, Corynomma* and nearly all luminous Myopsids with the so-called ink-sac organs). However, the two organs of *Onychoteuthis* do not make a pair, they differ in size as well as in position, the smaller organ being anal and the larger organ at the branchial level. *Lycoteuthis, Nematolamps, Lampadioteuthis, Pterygioteuthis* and *Pyroteuthis* have unpaired visceral organs besides paired ones, but they are mostly post-branchial in position. Although we are still in controversy as regards the affinity of the photogenic organs between *Onychoteuthis* and other luminous cephalopods, only the intra-pallial band-like organ of *Ornithoteuthis volatilis* can be considered here. In this squid as already described in the previous paper the organ appeared in the shape of a long narrow band in the middle of the visceral mass from the midrectal level to the posterior end with two thickennings throughout the length, one near the anterior end between anal openning and gills and the other at the branchial level (Okada 1968, p. 85, fig. 3 B). Here it may be considered that the narrow posterior band behind the branchial node has disappeared and the remaining two thickennings shift to the left side of the rectum or the rectum itself moves to the right side without chaning the original position of the thickennings. That they come to a close associa-

tion with the ink-sac is a matter of subsequent consequence.

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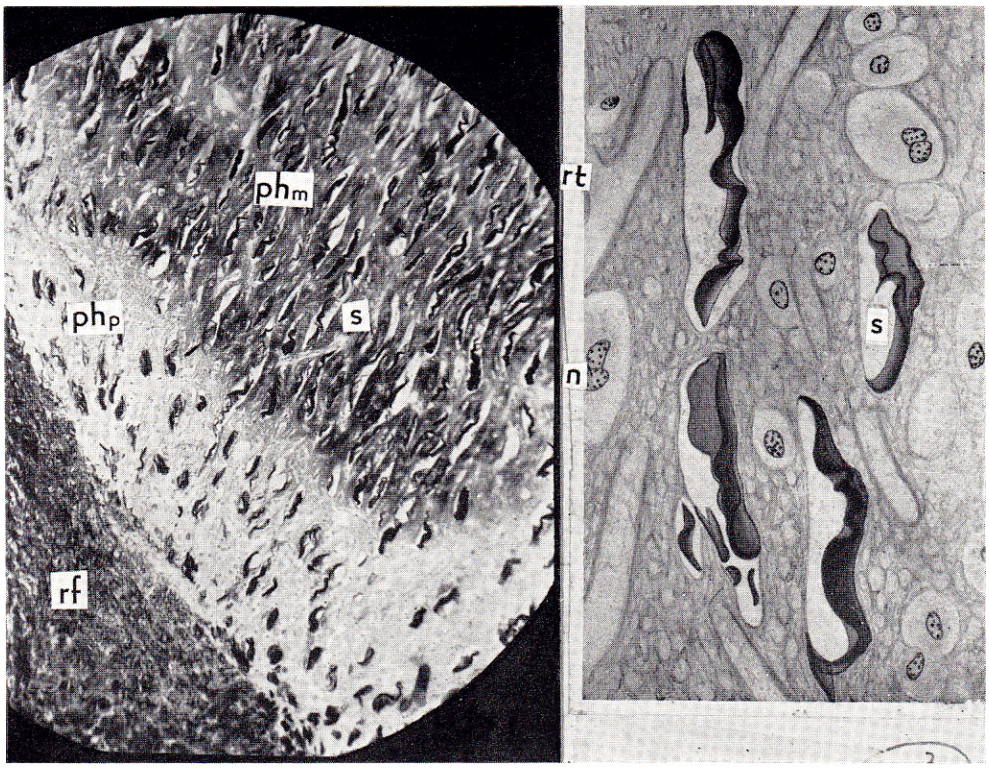

図版説明　Explanation of plate

1. 北日本ツメイカ発光組織の一部拡大，約 100 倍
   Part of the photogenic tissue of *Onychoteuthis borealijaponica* in magnification, ×ca. 100
2. 同発光組織の中央部をさらに拡大したもの，430 倍
   Still higher magnifidation of the median part of the photogenic tissue, ×430

図に使用した省略文字　Abbreviation used in jigures

an	anus （肛門）
ant	anterior （前方）
bl	blood vesseel （血管）
cm	commissure （連絡帯）
cp	capillary （毛細血管）
g	gill （鰓）
ik	ink-sac （墨汁嚢）
in	intestine （腸）
int	intermediate layer （中間層）
l	lens or left （水晶体または左）
ms	muscle （筋）
n	nerve or nucleus of cell （神経または細胞核）
ph	photogenic tissue （発光組織）
phm, *php*	median and peripheral pasts of the photogenic tissue （発光組織の中央および周辺部）
post	posterior （後方）
r	right （右）
rf	reflector （反射層）
rt	endoplasmic reticulum （発光組織内の網状構造）
s	scaly lamellae （鱗状薄片）