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# BIOLOGICAL BULLETIN

## LIGHT PRODUCTION IN CEPHALOPODS, II.

### An Introductory Survey.

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## 5. Color and Intensity of Light.

But little is known concerning the color, particularly what may permissibly be termed the *intrinsic* color, of the light produced by cephalopods, in fact next to nothing of any of its fundamental physical qualities. This of course follows as a natural corollary of the scanty nature of the recorded human observations of these animals in the living state. Such as they are the appropriate data gleaned from the preceding section of this paper are briefly tabulated.

Vérany's observations previously quoted are a little ambiguous and it is not just evident whether the "sapphire blue" and "topaz yellow" rays which he describes with such naïve enthusiasm for the photophores of *Histioteuthis* apply to the result of their functional activity at night, or merely to their ordinary brilliant coloration in the daytime. The fact that he was "blinded" would seem to indicate the former.

### Table IV.

Color of Light in Cephalopods.

| Species. | Date of Published Observation. | Color of Light. |
|---|---|---|
| Œgopsida: | | |
| Family Lycoteuthidæ, | | |
| *Lycoteuthis diadema* (Chun) | Chun, 1902 | ultramine, sky blue, ruby red, pearly white. |
| Family Enoploteuthidæ, | | |
| *Watasenia scintillans* (Berry) | Watasé, 1905, 1912. | |
| | Ishikawa, 1913 | clear blue. |
| | Sasaki, 1914 | Prussian blue to purplish. |
| Family Histioteuthidæ, | | |
| *Histioteuthis bonellii* (Férussac) | Vérany, 1851 | ? |
| Family Ommastrephidæ, | | |
| ? "*Loligo sagittatus* Lamarck" | Giglioli | ? |
| Family Cranchiidæ, | | |
| *Cranchia* sp. | Holder, 1887 | ? |
| Myopsida: | | |
| Family Sepiolidæ, | | |
| *Sepiola* sp. (*rondeletii* Leach ?) | Marchand, in Meyer, 1906 | ? |
| *Inioteuthis japonica* Verrill | Sasaki, 1914 | "cobaltish." |
| *Heteroteuthis dispar* (Guppell) | Meyer, 1906 | pale greenish. |
| | Dahlgren, 1916 | blue green. |
| Octopoda: | | |
| ? *Polypus* sp. | Darwin, 185 | ? |
| ? small octopod | Giglioli | "pale whitish." |
| Tremictopus gracilis (Souleyet) | Souleyet | ? |

Of the subsequent observations, only a few trouble to specify the apparent color of the light rays. I use the word apparent advisedly, not alone because of the ever-present subjective considerations by which one and the same ray may yield diverse impressions to different persons at the same time and under the same conditions, or to the same person at different times or under different conditions, but also because there is evidence that the original color values of the light rays may suffer modification, either by reason of the physical features of some of the supervening tissues of the photophore itself, or by the interposition of the chromatophoric color screens to which attention has already been drawn.

The extent to which the brilliantly varied illumination which was described by Chun for *Lycoteuthis diadema* is due to such considerations as these, rather than to differences inherent in the light rays produced by the respective organs is therefore a matter for considerable speculation. In this species Chun (:03, pp. 569–570; :03*a*, p. 81; :10, p. 50) described the light of the central organ in each subocular series as "marvelous ultramarine blue," of the anterior axial organ as "sky blue," of the two anal organs as "ruby red," of the remaining organs as "snow-white" or "pearly." But it should be remembered that no matter what other rays may have suffered absorption to result in the described effect on the human eye, no sort of screen or filter could manufacture those which evidenced themselves and they must therefore have been produced within the photogenic tissues. If, as in all other luminous organisms which have been subjected to examination, this is still a relatively efficient and therefore "cold" light, the question is yet before us whether the "ruby red" rays of *Lycoteuthis* are none the less as "cold" as the ultramarine and blue ones, or as the blue-green luminescence of the firefly. The biochemist and biophysicist have here a tempting field, once the technical biological difficulties of securing and handling the animals can be fairly overcome.

The light of the luminous secretion of *Heteroteuthis dispar* is described by Meyer (:06, p. 389) as "pale greenish," and by Dahlgren (:16, p. 71) as "the usual blue-green of luciferine when burning outside the body."

Sasaki and other observers of *Watasenia scintillans* describe the light of the large organs at the tips of the ventral arms as purplish or Prussian blue, the body organs appearing "whiter and less luminous" than these. In spite of their absolutely different histological structure, the rays emanating from the integumentary and subocular organs do not here appear to be respectively distinguishable and one wonders whether, in this regard, the observations recorded convey the whole truth.

That such elaborate variety in the size, morphological detail, and possession of accessory contrivances as will shortly be described, must find at least partial expression in differences in the physical qualities (intensity and color) of the resulting light rays, seems as inescapable to the present writer as it did to Chun (:03*a*, p. 81). And on the whole the scanty evidence just outlined is in accord, showing that the hues of the light are different, often most strikingly so, not alone as between independent species, but between the organs occupying different situations on the body in one and the same species.

## 6. Distribution of Photophores on Animal.

The photogenic function in cephalopods is, as has been seen, not a general attribute of the body surface, but is always, so far as is known, localized in the specialized tissue of definitely circumscribed organs disposed in equally definite regions of the body. It therefore becomes appropriate to examine what position or positions on the body these structures have come to occupy. Proceeding accordingly, one is at once struck with the fact that although strong evidence of partiality for certain special situations exists, yet no hard and fast rule may be laid down. The region where the organs occur most commonly seems to be by all means the surface of the ventral hemisphere of the eyeball. Photophores are found in this position in most (probably all) of the Cranchiidæ, in *Enoploteuthis*, *Abralia*, *Abraliopsis*, *Watasenia*, *Asthenoteuthion*, *Pyroteuthis* and *Pterygioteuthis* of the Enoploteuthidæ, in all the Lycoteuthidæ, in *Lampadioteuthis*, in *Ctenopteryx*, and in *Chiroteuthis*,—at least some 25 and more probably around 29 of the entire 44 photogenic genera in the suborder Decapoda. Most of the cranchiid genera, comprising, so far as known, the entire subfamily Taoniinæ, are peculiar in that the subocular photophores are reduced to one or at most two organs which are frequently so large as to cover nearly the entire lower surface of the eyeball. When two such are present they are semicircular or more or less crescentic in outline, the smaller or anterior organ fitting into the concavity of the larger. The eye-organ in *Ctenopteryx* is a single large falciform structure. In most genera, however, the subocular photophores are smaller and more diffuse in their arrangement, the commonest system being an alignment in a simple, bead-like, longitudinal series on the ventral periphery of the eyeball. Curiously enough, the series usually includes organs belonging to two or more diverse structural types. Such is the arrangement to be found in *Lycoteuthis*, *Nematolampas Abralia*, *Abraliopsis*, *Watasenia* and *Enoploteuthis*, the last-named genus having nine or ten organs on each eye, all the other genera five. *Liocranchia* and *Pyrgopsis* have four organs similarly located, but all of one type. *Chiroteuthis picteti* and *C. imperator* are figured by Chun as having three longitudinal chains of isomorphic organs, 22 to 29 in all, upon each eye. In the latter species he found the number to be somewhat variable, which is an unusual circumstance with the subocular organs. This is a particularly striking fact when the remaining five genera having this type of photophore are considered. In all of these, namely, *Lampadioteuthis*, *Pyroteuthis*, *Pterygioteuthis*, *Cranchia* and *Leachia* the photophores of the eyes, varying in number from four in *Lampadioteuthis* to fifteen in *Pterygioteuthis giardi*, have lost their simple serial arrangement, and the individual organs are scattered to a greater or less degree over the lateral as well as the ventral region of the eyeball. Their distribution thus becomes highly irregular, yet it is almost always absolutely definite and practically invariable within the bounds of each single species. *Chiroteuthis veranyi*, as described by Chun, is unique in having two large bands of photogenic tissue on the ventral convexity of each eye, accompanied by a few small isolated photophores of the more ordinary form, by the coalescence of a number of which they perhaps originated. Since the genera possessing subocular organs are all œgopsid, it follows that these photophores are covered by the double fold of the integument which forms the eyelid, and consequently in preserved specimens are often invisible without partial dissection. But in the Cranchiidæ the overlying membranes are thin, transparent, and very insufficiently equipped with chromatophores, so that in good specimens the organs may be clearly seen from the exterior. And likewise in certain other groups such as *Enoploteuthis* and the Abralioid genera, we find a delicate, transparent, elongate-oval "window" in the integument, nearly or entirely free of pigmented chromatophores, and overlying that portion of the eyeball where are borne the photogenic organs. There can be little doubt that this functions in aid of the latter by facilitating the passage of their rays.

The next most frequent topographic type of photophore to be met with comprises those occurring in the general integument of the body, primarily on the mantle, head, and arms. A remarkable peculiarity of the integumentary organs is that they, like the subocular photophores, are generally confined to the ventral aspect and this circumstance has given rise to some interesting theories regarding the origin and ecologic significance of the whole phenomenon of light production in this group of animals. Some writers have gone so far as to state that the distribution of these organs is *entirely* ventral, but this is not in strict accord with the facts, there being a few scattered photophores on the dorsal aspect of the mantle in such forms as *Abralia astrolineata* and most of the Histioteuthidæ, while Verrill's figures show them to be quite as strongly developed in this region in his *Mastigoteuthis agassizii*[14] as they are below. Certain other species of *Mastigoteuthis* have them in plenty on the dorsal surfaces of the fins, even if not upon the body proper. Again in Professor Joubin's anomalous *Melanoteuthis* the supposed photophores are entirely dorsal. The possibly photogenic tubercles of *Mastigoteuthis cordiformis* should likewise be recalled in this connection, and finally the presence of photophores on the dorsal arms of *Nematolampas* and *Benthoteuthis*. But even as many exceptions as this serve principally to accentuate the prevalence of the rule. In some genera the integumentary organs are developed on the

[14] *Bull. Mus. Comp. Zoöl.*, V. 8, Pl. I., 1881.

ventral surface of the mantle only (*Ancistrocheirus*, *Hyaloteuthis*, and, according to Chun, though he is controverted by other writers, *Chaunoteuthis*). In others (*Eucleoteuthis*) they occur on the ventral surface of the head as well. In *Calliteuthis*, *Histioteuthis* and some species of *Mastigoteuthis* they are found not only on the mantle and head, but on the aboral surfaces of the ventral and ventro-lateral arms. In *Mastigoteuthis agassizii* they are figured as occurring even on the tentacle stalks, as they do likewise in *Thelidioteuthis*, although this would appear to be an unusual situation for organs of the integumentary type. In the former of these two genera they are numerous in the integument of the head, arms, and mantle as well as the tentacles; in the latter, they are less numerous and although found along the outer side of the tentacles, occur elsewhere only on the ventral aspect of the mantle and head, where they have a very regular and characteristic arrangement. Finally in a number of well-known genera (*Enoploteuthis*, *Abralia*, *Abraliopsis*, *Watasenia*, *Mastigoteuthis*), integumentary organs are plentifully distributed in indefinite number over the entire ventral aspect of mantle, head, arms, and funnel.

On the fins these organs appear less frequently, but they are described as occurring dorsally in several species of *Mastigoteuthis*, and in one (*M. talismani*) on their ventral faces.

In a number of species there is a particular development of the integumentary photophores in the neighborhood of the eyes, usually in the form of a circlet around the margin of the lid opening, and such a circlet may occur, as in *Enoploteuthis*, *Abralia*, *Abraliopsis* and *Watasenia*, in addition to a well developed series of subocular organs. As a general rule, and certainly in the four genera named, the organs comprising this circlet are not to be distinguished from those of the general integumentary surface save by their peculiar arrangement and position. In the Histioteuthidæ, however, comprising the genera *Histioteuthis* and *Calliteuthis*, a most singular modification of this feature is encountered. A peculiar attribute of these genera is that, probably without exception, all the species have the left eye enormously more developed than the right, so much so in fact that a strong lateral torsion or displacement of the entire, in both genera relatively enormous, head is produced, which would seem to render it a physical impossibility for the animal to propel itself in a straight path without recourse to spiral movement or some violent sort of counter twisting. This asymmetry extends quite inexplicably to the photogenic organs, inasmuch as the "normal" right eye has a well developed circlet of photophores surrounding the lid opening as above described, while the Brobding nagian left eye has the photophores of its circlet not only pulled farther apart by the distention of the lid, but its every component reduced almost to a rudiment, some of them quite atrophied, or they may even be, as Sasaki has stated for *Calliteuthis separata*,[15] absent entirely. It seems as though from the very nature of the case there must be some correlation between such pronounced asymmetry and the habits of the animals, but no reasonable explanation of what might be necessary to bring about or to render advantageous such an anomalous condition seems ever to have been suggested. In *Mastigoteuthis glaukopis* there is no circumocular circlet of photophores, but a single photogenic organ is described as occurring in the ventral edge of each lid sinus.

In a few species the integumentaty photophores are few and consequently definite in number and position (*Ancistrocheirus*, *Thelidioteuthis*, *Hyaloteuthis*, *Eucleoteuthis*). This is probably true also of the very young or larval stages of all the species possessing photogenic organs, but in adults of most species, though still continuing to retain more or less evidence of the primal bilateral symmetry, they are apt to increase to such an extent as to become practically or quite impossible of separate identification and enumeration and thereupon show little constancy in either number or position.

*Eucleoteuthis* is a genus which deserves discussion by itself. It is unique among known cephalopods in that its photogenic organs instead of forming small rounded or ovoid capsules as in practically all the other genera, are developed as a pair of narrow, more or less interrupted stripes or bands of photogenic tissue extending along the ventral aspect of the mantle for nearly its entire length. A small oval tract of similar tissue flanks the

[15] *Journal College Agriculture Tohoku Imperial University*, V. 6, p. 137, 1915.

outer side of each band at its anterior end, and, in the type species at least, there is a pair of somewhat larger, transversely ovoid photogenic areas on the head at the base of each ventral arms. That these curious tracts should be classified with the remaining organs here collectively referred to as integumentary is by no means certain.

The arms are a favored situation for photogenic organs. The extension along their outer surfaces of the ordinary integumentary photophores in the case of such genera as *Enoploteuthis*, *Abralia*, *Abraliopsis*, *Watasenia*, *Calliteuthis*, *Histioteuthis*, and certain forms of *Mastigoteuthis*, has already been noted. In addition to this certain special types of organs are sometimes developed. One of the generic characters of *Chiroteuthis* is the presence of a series of conspicuous dark photophores along the oral aspect of each of the greatly enlarged ventral arms. *Nematolampas* has a small dark photophore embedded in the extreme tip of each arm of the two dorsal pairs. Not only this but each arm of the third pair bears immersed in its tissues along the outer margin a series of plainly visible photogenic organs which continue as the principal component of a long, chain-like, filamentous extension of the arm which in life must extend like a string of fiery beads far in advance of the animal. There are in excess of thirty individual organs in each chain, but the true number may be much greater as no specimens of the species still retaining these extraordinary structures entirely in their pristine state have yet been captured. In *Abraliopsis* and *Watasenia*, genera so closely allied to one another that one could with about equal ease be regarded as but a subgenus of the other, there are three large, black, bead-like photophores, with perhaps some smaller, more rudimentary ones, in close juxtaposition at the tips of each ventral arm. As previously related, these are known to give forth a brilliant light. Rudiments of similar organs correspondingly situated are known in at least one species of *Abralia*, another nearly related genus. This is *A. astrolineata* Berry of the Kermadec Islands. The curious deep-sea *Benthoteuthis* has a single photophore on the outer periphery of each arm of the three dorsal pairs near the base, and none elsewhere on the body, an arrangement wholly unlike that met with in any other cephalopod.

Until very recently photophores on the tentacles have been supposed to be of rare occurrence, but it has lately been shown that they do actually so exist in quite a number of diverse forms, having tended to escape observation by reason of being embedded so deeply in the fundamental substances of the tentacle stalk as to be quite invisible in preserved material unless thoroughly cleared or otherwise specially treated. In *Pyroteuthis* Vivanti and Mortara have recently established the presence of a series of four such organs in the stalk of each tentacle. I had not only independently made the same discovery in material from both the Atlantic and Pacific, but had likewise found that there is yet a fifth tentacular organ present, and that the same condition obtains as well in the nearly related genus *Pterygioteuthis*. *Lycoteuthis* and *Nematolampas* have two such organs in each tentacle stalk. *Lampadioteuthis* is unique in possessing not only a series of four photophores embedded in the stalk proper, but in addition tucked away at its very base, a single large spherical organ of peculiar structure which is quite invisible without extraction of the entire tentacle from its socket. Conspicuous tentacular photophores are also shown in Verrill's figures of his *Mastigoteuthis agassizii*,[16] but the inference seems to be, as has been indicated above, that these are simply of the ordinary integumentary type, as seems to be true also of the tentacular photophores in the genus *Thelidioteuthis*.

We now come to the class of photogenic organs which is perhaps the most distinctive of the Cephalopoda as compared with other luminous animals, and which, next to the subocular photophores, exhibits the most general distribution within the group. Included here are a large array of very diversely constructed photophores found in quite various situations upon the visceral mass within the pallial chamber. These one and all, however, except in the case of those myopsids which eject their luminous secretion through the funnel, must naturally depend in life upon the more or less complete transparency of the mantle tissues to permit the unobstructed emanation of their beams. In preserved specimens, as would be expected, they can rarely be seen without laying open the pallial chamber, whereupon they are

[16] *Bull. Mus. Comp. Zoöl.*, V. 8, 1881, pl.1.

generally easy to distinguish, many of them being of unusual size and often of conspicuous coloration, while the situations which they occupy are peculiarly limited and, within a given species, constant. By reason of this last fact the intrapallial organs may readily be subclassified into four series, (1) anal, (2) branchial, (3) gastric, and (4) axial. Such a classification, too, in spite of its obviously superficial foundation, is a convenient one. That it is at the same time in all respects a natural or phylogenetic arrangement is probably not true, and it will no doubt be greatly improved upon by the first worker who takes up the relationships of these organs in any sort of adequate detail.

The term anal organs is misleading, but has become so well established in the literature that I use it pending the invention of a more appropriate term. The photophores so classified appear usually as a pair of quite large, often very brightly colored organs of rounded or ovoid outline, lying on the ink sac on either side of the rectum, with which they would otherwise appear to have no particular connection. Being often situated just back of the funnel, or sometimes almost within it, they are therefore sometimes termed the siphonal photophores, a name which in its turn is open to objection as inappropriate to the actual morphological relationships involved. Anal organs occur in a considerable number of little related genera, and the discharging photophores of the luminous Sepiolidæ are noteworthy for occupying an analogous situation.

The branchial organs are always paired, being situated one near the base of each gill. They are confined, so far as known, to the Lycoteuthidæ, Lampadioteuthidæ, and the pterygiomorph section of the Enoploteuthidæ.

The gastric and axial organs are classed together by most writers under the general term abdominal, but I prefer to separate the mesially situated, unpaired organs, which are often extended into a considerable series in the hinder portion of the mantle cavity, from the paired organs which sometimes occur near the middle of the body on either side of and often in close association with the anteriormost of the axial organs. There is evidence that in at least some genera the division here postulated into the paired gastric and unpaired axial organs is founded upon a good morphological as well as merely topographical basis, but at the same time it is impossible to emphasize too strongly that we are here dealing primarily with the mere somatic distribution of the organs, and not with a true genetic classification based on the embryology or finer anatomy, save where the latter becomes incidentally involved. The need for this qualification has no doubt already been patent to the reader from the foregoing discussion.

Of the dozen genera listed in the synopsis as possessing intrapallial photophores, only *Heteroteuthis*, *Sepiola*, *Euprymna*, *Chiroteuthis* and *Corynomma*[17] are described as having anal organs only, a single pair or organ formed by the fusion of a pair being present in each instance. *Lampadioteuthis* has paired anal and branchial organs (the latter very large) and a single posterior axial organ. *Pterygioteuthis* has paired anal and branchial organs, and four axial organs, the most anterior of which is vastly the largest, the most posterior very minute and pushed far down past the fins into the sharp-pointed tip of the body. *Pyroteuthis* has a quite similar illumination system, but the foremost axial organ is more anterior in position, is only a little larger than the others, and is flanked on each side by a small gastric organ. *Lycoteuthis* and *Nematolampas* have a single pair each of anal, branchial and gastric organs as above, a small anterior axial and a very large posterior axial organ. Branchial, gastric and anterior axial organs are placed at about the same transverse plane so that they form a belt of fiery jewels near the middle of the body. *Onychoteuthis* (*banksii*) is unique in having but two large unpaired photophores, both of which are intrapallial and lie upon the ink sac in the median line, one very large and ensconced in a specially constructed depression on the ink sac proper, the smaller upon the narrow, neck like, anterior portion of the sac.

The minute unpaired organs which have been mentioned as occurring in the spine-like tip of the body in *Pterygioteuthis* and *Pyrotheuthis* are probably correctly interpreted as but the terminal members of an unusually developed axial series. Lo-

[17] Chun rather doubtfully adds *Octopodoteuthis* to this list.

cated in the same general region as these, and, by their appearance, seeming to bear a closer relation to the intrapallial organs than to the other systems outlined, yet scarcely to be regarded as lying actually within the mantle cavity, are the conspicuous paired photophores placed at the extreme posterior tip of the body in *Nematolampas*. *Lycoteuthis* does not possess them. They stand in a class quite by themselves at present, but if the peculiar swellings to be noted in the same situation in certain species of *Abralia* are susceptible of a photogenic interpretation, or if Chun's identification of the posterior disk of *Spirula* as a luminous organ be accepted, a further extension of this division of the classification is afforded.

### 7. Structure of Photogenic Organs.

Another most remarkable feature of the development of photogenic systems in Cephalopoda is, so far as I am aware, the quite unparalleled variety of structural type manifested by their constituent organs. It is entirely beyond the scope of this paper to enter into any extended account of the histological detail, but it will be useful to call attention to at least a few of the main features. Suffice to say that since the first observations on the finer morphology of cephalopod photogenic organs made by Joubin in 1893, a most bewildering variety of structure within the confines of this single, narrowly limited group of animals has been brought to light, ranging all the way from the simple discharging glands of the luminous myopsids, and the lump of photogenic tissue which forms the proximal photophore in the tentacle of *Lycoteuthis*, through almost innumerable intermediate types, to the astonishingly complex bull's-eye lanterns of *Abraliopsis* and the mirrored searchlights of the Histioteuthidæ. Each species has in fact its own peculiar modifications and sometimes many of them. The histology of all affords a fruitful field of investigation, which, with all due respect to the fine work of Chun, Hoyle and Joubin, we can truly say has been hardly skimmed. This is especially true of the embryology and he who attempts to work out the origin and homologies of even the simplest of these organs will have a virgin field.

Cephalopod photophores appear only rarely to be made up of masses of photogenic tissue without accessory structures (intrapallial organs of Sepiolidæ; proximal tentacle organs of *Lycoteuthis* and *Nematolampas*; eyelid organs of *Mastigoteuthis glaukopis*). As a general rule they are more or less complicated.

The principal division of the organs on morphological grounds is that already noticed which places the discharging glands of the Sepiolidæ on the one hand,—the enclosed glands of the remaining photogenic genera on the other. The latter it is again possible to roughly separate into three types: the no doubt relatively primitive invaginated epithelial organs of which the subocular photophores of *Cranchia*, *Liocranchia* and *Leachia* are interesting examples, band-like expanses of photogenic tissue as in *Eucleoteuthis*, and the spherical, ovoid or discoid organs, often provided with the most extensive array of accessory mechanisms, which are found in most of the other genera.

The organs of the last mentioned class in their highest development attain to an almost unbelievable degree of complexity To the primary photogenic tissue, with its invariably abundant blood and nerve supply, are here added more or less efficiently developed reflector mechanisms, pigment cups, lenses, diaphragms directive muscles, mirrors, windows, color screens,—even in some cases accessory photophores, giving rise to the puzzling "double organs" which are met with now and then in the most dissimilar situations, so that their purpose and manner of functioning is left even more than it otherwise would be a complete enigma. In some cases only certain ones of these accessory structures are developed, in other cases nearly all, as in the miniature searchlights which yield such beautiful microscopic preparations in the integument of the Abralioid and Histioteuthid forms. Space will not permit a complete description, but the presentation of these various accessories in outline form will give an idea their wonderful variety and serve likewise as a convenient summary. The student desiring more detailed information is referred to the works cited in the bibliography, particularly those of Joubin ('93, '93*a*, '93*b*, '93*c*, '94, '95, :05, :05*a*), Hoyle (:02, :04, :09), Meyer (:06, :08), Vivanti (:14), and the beautiful memoirs of Chun (:03*a*, :10).

## Table V.

Component Parts of the Cephalopod Photophore.

I. Primary (photogenic tissue).
 1. Photogenic cells.
 2. Veins and arteries.
 3. Nerves.
 4. Connective tissue.

II. Secondary (accessory structures).
 1. Pigment cup (almost always present, but sometimes lacking where photophore is surrounded by other pigmented tissue, as the ink sac or eyeball).
  (*a*) Chromatophores.
  (*b*) Specially modified pigment cells (an adaptation of preceding ?).
 2. Reflector, or Tapetum.
  (*a*) Nucleated cells.
  (*b*) Fibers.
 3. Scale cells, or "Schuppenzellen" of Chun.
  (*a*) as reflector.
  (*b*) as lens or cornea.
  (*c*) in photogenic tissue.
 4. Lens.
  (*a*) Fibrillar.
  (*b*) Cellular.
   (1) Connective tissue.
   (2) Modified mantle musculature.
 5. Diaphragm.
  (*a*) Chromatophores.
  (*b*) Muscles.
 6. Window.
 7. Mirror.
 8. Accessory photophores ("double organs").

The duplex photophores deserve a further word. These comprise two separate masses of photogenic tissue so closely associated together that the conclusion seems unavoidable that in some way they function in common. Organs of this type seem to have been first discovered by Chun, who described them in some detail for a number of species. There is small doubt that histological examination will show the occurrence of similar organs in many other instances also. The double crescentic subocular photophores of certain Cranchiidæ have been briefly described on an earlier page. *Lycoteuthis* (and most probably *Nematolampas* also)[17] possesses a number of duplex organs, the

[17] *Nematolampas* certainly agrees in having the terminal subocular photophores equipped with an accessory photophore. The other organs mentioned have not yet been investigated.

distal organs of the tentacles, the terminal members of the subocular series, and the gastric organs, all being of this category. In the gastric organs, the respective masses of photogenic substance, though entirely distinct from one another, are contained within the same capsule. In the case both of these and the terminal subocular organs, which are separated, the accessory photophore lies beneath the principal one and the rays which emanate from it must accordingly pass through the latter if they are to have egress at all. In *Pterygioteuthis* the branchial organs are duplex, the accessory organ being contained a little to one side of its principal, but still within the same pigment cup.

### 8. Polymorphic Nature of Photogenic Organs.

The question is now very near, whether so many simple and elaborate morphological types of light-producing organs have any especially closer genetic relationship to one another where they are found within one and the same species or genus. And this leads easily to another, whether the photophores of any given species exhibit such manifold structural diversity as to render improbable their ultimate reduction to a single primordial type. The affirmation of this latter question implies the negation of the former, and I think we may certainly say that this seems most truly to express the facts as we have them. The accompanying table (Table VI.), which it has seemed worth while to elaborate upon the basis of the interesting outline given given by Chun, shows that whereas about a third of the genera cited each possess photophores belonging to a single general type, nearly as many have strongly dimorphic photophores, and an even greater number have trimorphic or polymorphic organs. It is nothing unusual therefore to find organs of extreme simplicity functioning as components of the same photogenic system which contains also organs exhibiting the most varying degrees of complexity in structural plan. While this seems to take place almost in hit or miss fashion, I think it may be taken as a general statement of fact that those species having a relatively abundant development of integumentary photophores distributed over the body generally fail to evolve a great variety of other types, the Abralioid genera providing the nearest to an exception to this rule (see Table VII.). Those species showing the richest development of structural type in general are the ones which depend upon intrapallial rather than integumentary organs to serve the light producing function. Here there is sufficient divergence among the various organs as to discourage almost at a glance any attempt to homologize them on the basis of reference to a single primal type. Not only their diversity, but their extremely sporadic appearance in connection with organs and tissues of heterogeneous origin, is strongly inhibitive of any such view.

## Table VI.

### Polymorphism in Cephalopod Photophores.

| | |
|---|---|
| I. Genera with Isomorphic Photophores. | |
| *Thelidioteuthis* | Integumentary. |
| *Histioteuthis* | " |
| *Calliteuthis* | " |
| *Benthoteuthis* | On arms. |
| *Mastigoteuthis* | Integumentary. |
| *Cranchia* | Subocular.[18] |
| *Liocranchia* | Subocular. |
| *Pyrgopsis* | " |
| *Hensenioteuthis* | " |
| *Bathothauma* | " |
| II. Genera with Dimorphic Photophores. | |
| *Enoploteuthis* | Integumentary; subocular. |
| *Leachia* | Subocular. |
| *Megalocranchia* | " |
| *Crystalloteuthis* | " |
| *Toxeuma* | " |
| *Taonidium* | " |
| *Corynomma* | Subocular (?); intrapallial. |
| III. Genera with Trimorphic Photophores. | |
| *Abralia* (except *A. astrolineata*) | Integumentary; subocular (latter dimorphic). |
| *Chiroteuthis* | On ventral arms; subocular; intrapallial. |
| IV. Genera with Polymorphic Photophores. | |
| *Lycoteuthis* | In tentacles; subocular; intrapallial; 10 types (13 if 3 types of accessory organs are counted separately). |
| *Nematolampas* | In arms; in tentacles; subocular; intrapallial; at tip of body; probably 12 or 13 types (15 or 16 if accessory organs are counted separately). |
| *Lampadioteuthis* | In tentacles; subocular; intrapallial;—probably 7 or 8 types. |
| *Abralia astrolineata*, *Abraliopsis*, *Watasenia*, | Integumentary; tips of ventral arms; subocular (dimorphic). |
| *Pterygioteuthis* | Tentacular; subocular; intrapallial;—8 types. |
| *Pyroteuthis* | Tentacular; subocular; intrapallial;—probably 8 or more types. |

[18] Unequal in size, but showing clear structural evidence of homology.

# TABLE VII.

## DETAILED OUTLINE OF OCCURRENCE OF POLYMORPHIC PHOTOPHORES IN CEPHALOPOD GENERA.

| | *Lycoteuthis diadema.* | *Nematolampas regalis* | *Lampadioteuthis megaleia.* | *Abralia astrolineata.* | *Abraliopsis* sp. | *Watasenia scintillans* | *Pyroteuthis margaritifera.* | *Pterygioteuthis gemmata.* | *Pterygioteuthis giardi.* |
|---|---|---|---|---|---|---|---|---|---|
| Integumentary: | | | | | | | | | |
| Dorsal surface of mantle | – | – | – | +(1) | +(1) | +(1) | – | – | – |
| Ventral surface of mantle | – | – | – | + | + | + | – | – | – |
| Ventral surface of funnel | – | – | – | + | + | + | – | – | – |
| Ventral surface of head | – | – | – | + | + | + | – | – | – |
| Ventral arms | – | – | – | + | + | + | – | – | – |
| Circumocular | – | – | – | + | + | + | – | – | – |
| Subocular: | | | | | | | | | |
| Ventral periphery | 10(3) | 10(3) | 6(2?) | 10(2) | 10(2) | 10(2) | } 24(3) | 28(4) | 30(4) |
| Lateral | – | – | 2 | – | – | – | | | |
| Arms: | | | | | | | | | |
| Tips of dorsals | – | 2 } (1?) | – | – | – | – | – | – | – |
| Tips of dorso-laterals | – | 2 } | – | – | – | – | – | – | – |
| Ventro-laterals | – | 62+(1) | – | – | – | – | – | – | – |
| Tips of ventrals | – | – | – | 6(1) | 6+(1) | 6+(1) | – | – | – |
| Tentacles: | | | | | | | | | |
| At base | – | – | 2(1) | – | – | – | – | – | – |
| Along stalk | 4(2) | 4(2) | 8(1) | – | – | – | 10(1) | ? | 10(1) |
| Intrapallial: | | | | | | | | | |
| Anal | 2(1) | 2(1) | 2(1) | – | – | – | 2(1) | 2(1) | 2(1) |
| Branchial | 2(1) | 2(1) | 2(1) | – | – | – | 2(1) | 2(1) | 2(1) |
| Gastric | 2(1) | 2(1) | – | – | – | – | 2(1) | – | – |
| Axial | 2(2) | 2(2) | 1(1) | – | – | – | 4(1) | 4(1) | 4(1) |
| Posterior tip of body | – | 2(1) | – | ? | – | – | – | – | – |
| Total number photophores | 22 | 90+ | 23 | 16+∞ | 16+∞ | 16+∞ | 44 | 36(+?) | 48 |
| Probable number structural types | (10) | (12 or 13) | (7?) | (4) | (4) | (4) | (8) | (8?) | (8) |

The photogenic systems of all the species of the eight genera having polymorphic organs are outlined in further detail in Table VII. Those species considered having the mere largest number of photophores are the three Abralioids, occupying the three central columns of the table, but those exhibiting the highest degree of polymorphism are *Lampadioteuthis megaleia*, which has not been investigated histologically but must have not less than seven or eight types of photophores in all, *Lycoteuthis diadema*, with ten types, or thirteen, if the accessory organs are counted in, and *Nematolampas regalis*. *Lycoteuthis diadema*, with the immeasurable advantage of having had its marvelous photogenic properties observed in the living state, is usually cited as the example par excellence of a luminous cephalopod. However, it is evident from sheer morphological grounds that even this wonderful creature must yield the palm to another, if nearly related, genus and species,—the truly amazing *Nematolampas regalis* of the Kermadec Islands. Whether this species will ultimately be found to display all the varied brilliance of the red, white, and blue lights of *Lycoteuthis*, the fact remains that in addition to a complete series of exactly homologous organs, it has an entire battery of pyrotechnic engines of its own, so there is every reason to expect a more rather than a less elaborate illumination. The total number of photophores in this species is in excess of ninety, which are elaborated upon no less than twelve or thirteen different structural principles of uncertain homologies with one another. Counting in the three types of accessory photophores which are to be found in the eight "double" organs (proximal tentacular, terminal subocular, and anal), the total number of types is increased to fifteen or sixteen. Which of the alternative figures quoted is the correct one is still to be established by histological work.

### 9. Systematic Significance of Photogenic Organs.

It follows almost as a corollary from what has been said in the foregoing sections of this paper that the photogenic system evinces a complex of features of the utmost value to the taxonomist. Of late years ever increasing weight has been given to it, and the presence of constant differences, even though minute, in its components, is now admitted practically without debate as ample ground for taxonomic discrimination. Where such differences are shown to occur, further differences in the remaining organization seem practically predestined for eventual discovery. Good characters for specific discrimination are to be found, not only in the presence or absence of photogenic organs, but also in their distribution on or within the body, in their number, in their size, and in the veriest details of their intrinsic structure. The taxonomist has in fact few more convenient points of attack in the pursuit of his primary objects of classification and relationship than that afforded by the light organs. And this is exactly what we find, if to somewhat less degree, among the fishes and the few other groups where the photogenic organs have attained some considerable complexity. One can construct a fairly workable taxonomic key based on the photogenic organs alone, for such species as possess them.

## 10. Probable Polyphyletic Origin of Photogenic Organs.

Before concluding this paper a somewhat general answer may be attempted to a question which has no doubt occurred more than once in the mind of the reader, and which indeed has been touched upon very nearly on more than one occasion—Is photogenesis a primitive function among cephalopods? In other words, are our present day species descended from an ancestral photogenic stem, some branches of which have now yielded up the function? Or has photogenesis arisen several times in this class of animals, possibly to meet altogether diverse conditions or associations in the environment, so that its presence therefore becomes of secondary rather than primary significance?

At first glance the widespread distribution of the function in the great and, comparatively, primitive œgopsid group of cephalopods favors an affirmative answer to our first query. But in reply to this it may be said that the varied pelagic environment of these forms would almost per se favor the development of the light-producing function after a manner which would be hardly likely to hold true among the more littoral Myopsida and Octopoda, the former of which are mainly frequenters of much shallower water than the Œgopsida, the latter hardly ever pelagic at all, and then generally surface forms or confined to the shallower water like so many of the myopsids.

There are many other arguments which may militate against any theory of monophyletism and as strongly support the contrary view as brought out by the last query above. These, having already been largely elaborated elsewhere or to be dealt with in another connection later on, need be merely summarized here. Such considerations are:

1. The uneven distribution of photogenic organs throughout the entire group, and, as a corollary of this, their appearance in distantly related groups more or less sporadically.

2. The variety and sporadic character of the development of photogenic organs in different regions of the body.

3. The large number of strongly diverse structural types.

4. The evidence from ecological considerations, the distribution upon the body, and similar facts that these organs have arisen in response to very diverse environmental requirements.

How then may one bespeak a photogenic *system*? Exactly as one speaks of a muscular system, or a skeletal system, or a receptor system in almost any animal body. The term is used in the sense not necessarily indicating an aggregation of homologous structures, but an assemblage of organs within a single organic body exhibiting more or less similar or cöordinate physiological reactions, if at times neither in fact phylogenetically nor ontogenetically related.

## 11. Concluding Note.

This paper is mainly a compilation from the scattered work of other authors. No doubt there are omissions, but the aim has been to present simply a concise summary of the knowledge of this subject which has been gained to the present time. It cannot be too strongly emphasized that not only are many more species of luminous cephalopods likely to be discovered in the future, but some of those now known but not yet recognized as possessing photogenic properties are likely to be revealed as having them. Of the known luminous forms some will no doubt prove to possess luminous organs or properties additional to those described. Bearing all this in mind, if this little paper but furnishes some delving student just a little better base of attack on his problem than might otherwise have been afforded him, its purpose will have been fulfilled.

## 12. Summary.

1. Light production is an unusually widespread phenomenon in the molluscan Class Cephalopoda.

2. Although unknown in the Order Tetrabranchiata, scarcely developed in the octopod section of the Dibranchiata, and occurring little more than sporadically among the Myopsida, over one half of all described Œgopsida are known to possess photogenic properties.

3. The actual production of light by living cephalopods has been observed only rarely, but in species of sufficiently diverse relationship to confirm the evidence drawn from the morphology and histology of organs found in the remaining species.

4. The light of some species exhibits remarkable brilliance.

5. The color of the light emanating from the respective organs within the same species or in different species may exhibit striking differences in both intensity and quality, but it is not known to what extent this is actually due to inherent diversity in the physical properties of the light rays themselves.

6. Photogenic organs may occur in almost any portion of the body in this group of animals, but the outer integument, eyeball and pallial chamber are the situations most favored. They are often internal and able to function only by reason of the transparency of the body tissues in the living state.

7. The organs are predominantly, but by no means exclusively, ventral in distribution.

8. The organs are strongly polymorphic, even in the same species, varying from comparatively simple bodies of photogenic tissue to the highly complex "searchlight" types.

9. Numerous duplex organs, or organs with accessory photophores, are known to occur.

10. Luminous organs in the Myopsida are usually of the type known as discharging. Those of the other groups are entirely of the enclosed or ductless type.

11. The maximum polymorphism in the photophores of any

single species occurs in *Nematolampas regalis* Berry, from the Kermadec Islands, where the 90 or more organs are elaborated upon 12 or 13 more or less diverse structural principles.

12. The occurrence, distribution, arrangement, and morphological detail of photogenic organs in cephalopods are features of considerable taxonomic importance and yield valuable clues as to the relationship and classification of the genera and species even where still unknown anatomically.

13. The best evidence seems to indicate that the photogenic organs in this group of animals are polyphyletic and more or less sporadic in origin, hence that light production in cephalopods is not an essentially primitive or ancestral function to be regarded as now lost in many members of the group.

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