LIGHT PRODUCTION IN CEPHALOPODS, I.

An Introductory Survey.

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Contents.

1. Introduction.

Recent interest in the subject of biophotogenesis has been so great, and bids so fair to continue at high ebb, until at least the problem of the economical artificial production of chemical light has been solved, that for the use of the many classes of investigators, most of whom are not zoölogists and can scarcely be expected to possess accurate taxonomic knowledge of the group with which they may chance to wish to work, it would be exceedingly desirable if there could be placed on record in compact form a summary of all the species of each principal division of plants and animals which are known or thought to possess photogenic properties. The writer's desire to see this service performed on behalf of the cephalopods, animals which must always stand well up with the highest in the estimation of the student of organic light, furnished the initial stimulus which has finally broadened into the production of the present paper. As a taxonomist, however, and, in so far as this particular group of animals is concerned, one of that despised species, the "closet naturalist"—he can only go a certain way with his subject, and by the same token, his remarks must perforce have only a very limited value. Yet the effort seems worth while spending, and he can fairly plead in extenuation of his temerity, if not of his own limitations, that cephalopods are such active, delicately balanced creatures, and so exquisitely adjusted to an environment in which it is next to impossible to observe them accurately, and which it is even more vain to attempt to establish, even partially, under artificial conditions, that the difficulties of subjecting the details of their life history and ecology to that searching examination required by the standards of modern biological investigation have proven practically insurmountable. Therefore the unfortunate circumstance that we have no specialist in this branch,—no authoritative student of the bionomics of cephalopods, and that such halting summarization as can be done must be handled by the systematist or general student of the group, if at all. Admitting then the largely pragmatic and temporary rather than permanently intrinsic value of the present dissertation we may proceed with it, for even so small a contribution as this can pretend to be should prove helpful.

Amid the wealth of remarkable features, structural and physiological, with which the entire group of the Cephalopoda entices the student, the variety and multiplication of those which in an earlier day would have been as unquestioningly as delightedly hailed as *adaptive* are supremely conspicuous. These are special for the most part to the conditions and vicissitudes brought about by an exceptionally active manner of life in an environment full of actual or potential diversity. Not even the fishes are better swimmers, nor, with all their aristocratic vertebrate organization, lead a more complicated struggle for existence. It is perhaps concomitantly both a result and cause of all this that the group so fairly teems with bizarre cells, tissues, organs, complexes of organs, which, as we may as well admit without further parley, can scarcely be interpreted otherwise than as marvelously exquisite adaptations, each to its own definite end. Such knowledge of most of these as we possess has been amassed almost wholly since the time of Darwin, else the pages of the

"Origin" might have been enriched by many examples as startling in their way as any of the classical ones. The complex cephalopod chromatophore, the inter-playing system of exactly balanced musculature with scarcely any hard skeletal parts to give it support and leverage which goes to make up the arms and each single sucker, the delicate adjustment between eye, sucker and chromatophore through the mediation of the nervous system to result in one of our most perfect demonstrations of concealing coloration, the innumerable types of hectocotylus often involving the most astonishing modifications in sexual behavior, the amazing and still insufficiently understood mechanism of the spermatophore, the eyes, and, without attempting to prolong the list further, the photogenic organs,—each is in its own way a triumph of adaptive development, how much so we may perhaps infer to some extent from the widespread occurrence of these structures in one form or another among nearly all the now-surviving cephalopods. Continuing with the structures last named, for instance, I think it can be truly said that no other class of animals can compare with the cephalopods in the complexity, diversity, beauty, brilliancy,—in brief, the high specialization of organs devoted to the production and utilization of that form of energy which to our human faculties finds expression as light.

It has been said with considerable show of truth that the generation of light by the plasm of animals and plants is really far less to be marveled at than the transformation of their energy into motion. But motion is practically a general property of protoplasm in all its forms, without which it could scarcely exist as living substance at all. The reason why the production of organic light appears so remarkable to most of us is more special: it is partly of course because of the apparent economy of this light so far as the dissipation of heat energy is concerned, but mainly to the average observer because of its evident highly specialized adaptation to certain particular ends.

Dubois wrote in 1895:[1] "The most resplendent of all animals are *insects*, of which class the glowworm, beloved of the poets, is one of the most brilliant examples." Cephalopods were scarcely

[1] Smithsonian Report, 1895, p. 418.

noticed as being luminous at that period, but now we know that the firefly and glow-worm pale in comparison, and that probably not even the brilliant display of the tropical elaters can vie with the gorgeous pyrotechnics of certain squids. It is indeed quite possible that the latter exhibit the highest development of the photogenic function known in the entire animal kingdom.

2. Classification of Cephalopods.

Living members of the Molluscan Class Cephalopoda cleave simply and naturally into two well-defined, easily separable groups. The first of these, and that universally regarded as the most primitive, is the Order Tetrabranchiata, comprising only the few species contained in the single genus *Nautilus*. The animals of this group are characterized especially by the possession of a massive, chambered, external shell; of a "funnel" formed by the appression of two lateral folds which remain unfused in the median line below; of a system of suckerless lobes around the mouth, bearing retractile, annulated tentacles; of such traces of metamerism as the presence of two pairs each of ctenidia, "branchial hearts," auricles, renal organs, and osphradia; and of a simple "pin-hole" eye, open to the exterior. Ink-sac and chromatophores are absent.

The second group, Order Dibranchiata, comprising all living cephalopods except *Nautilus*, is characterized by either the complete atrophy of the shell or its reduction in the adult to a concealed loose coil (Spirulidæ), a calcareous plate (Sepiidæ), or a horny pen; by an entire, tubular funnel; by the development of the anterior portion of the primitive foot into a series of eight or ten muscular, sucker-bearing, tentacle-like arms about the mouth; by but a single pair each of ctenidia, branchial hearts, auricles and renal organs; by the presence, at least typically, of highly developed eyes; by the development of complex, specialized pigment cells in the skin; and by the presence of the peculiar "ink-sac." Osphradia are absent.

The Dibranchiata in their turn are sharply divisible into two subgroups, the Decapoda and Octopoda. The former are mainly pelagic; have finned, generally elongate bodies; have not only the eight "primary" arms of the octopods, but a pair of specially modified "tentacles" as well; have the suckers pedunculate, reinforced with a chitinous ring, and often very curiously modified; and have a so-called buccal membrane surrounding the mouth.

The Octopoda are principally shore or bottom-loving forms; short bodied; lack fins, or have them only secondarily developed; have eight arms only, with their suckers sessile and lacking chitinous rings; and lack the buccal membrane. There are also important internal characters which need not concern us here, but it may be said that few living groups are more sharply delimited. As a whole the group of the Decapoda has seemed to most students more archaic than the Octopoda, at any rate is less uniformly divergent from what must have been the ancestral stock, but it includes many highly specialized types, and probably neither group as we now know it can be taken as especially "primitive."

Of the two groups the Decapoda are much the less uniform, and are therefore still further to be divided. The classical bifurcation, which has found general acceptance until quite recently, is that of d'Orbigny, into Œgopsida, or those forms in which there is a free eyelid, and the Myopsida, in which there is a simple fold-like pseudo-lid, or the skin passes uninterruptedly over the eyeball. There seems to be no doubt but that the Œgopsida, at least, form a monophyletic, natural group, for on this point there is reasonable agreement. This cannot be said of the Myopsida.

The principal alternative system is that of Naef (1916).[1] He sets apart the Sepias and Sepiolids together as one of the two main subgroups, the Sepioidea. The other group, which not altogether satisfactorily he denominates Teuthoidea, is subdivided into Myopsida (here restricted by the elimination of the Sepioidea and hence comprising only the single family Loliginidæ) and Œgopsida, the latter as outlined above. Naef's classification avoids several very serious difficulties involved in the standard arrangement, but encounters, perhaps, certain others, which need not be dwelt upon here.

For convenience the two systems are summarized in the

[1] Naef, A. J., *Pubblicazione Stazione Zoologica Napoli*, V. 1, pp. 14–17, 1916.

accompanying table, that of Naef being slightly modified from his printed synopsis in order better to serve the purposes of the moment.

STANDARD SYNOPSIS OF THE CLASS CEPHALOPODA.

Phylum MOLLUSCA.
  Class CEPHALOPODA.
    Order I. *Tetrabranchiata.*
      Suborder 1. *Nautiloidea.*
    Order II. *Dibranchiata.*
      Suborder 1. *Decapoda.*
        Division A. *Œgopsida.*
        Division B. *Myopsida.*
      Suborder 2. *Octopoda.*
        Division A. *Pteroti.*
        Division B. *Apteri.*

SYNOPSIS OF THE CLASS CEPHALOPODA ACCORDING TO NAEF.

Phylum MOLLUSCA.
  Class CEPHALOPODA.
    Sub-class I. *Tetrabranchiata.*
      Order 1. *Nautiloidea.*
    Sub-class II. *Dibranchiata.*
      Order 1. *Decapoda.*
        Suborder A. *Teuthoidea.*
          (*a*) *Teuthoidea myopsida.*
          (*b*) *Teuthoidea œgopsida.*
        Suborder B. *Sepioidea.*
      Order 2. *Octopoda.*
        Suborder A. *Pteroti.*
        Suborder B. *Apteri.*

In number of families and genera now living, the Œgopsida easily preponderate, but the tremendous modern development of the genera *Polypus*, *Sepia* and *Loligo* throws the preponderance in species over to the side of the Myopsids (+ Sepioids) and Octopods. For instance, among recent Cephalopoda are to be recognized some 32 families, and in round figures about 120 genera and 600 species.[1] Of these the Œgopsid Decapods claim 16 families (one half the total), 66 genera (slightly over one half), and around 175 species (nearly one third). The Myopsid (+ Sepioid) Decapods account for but 7 families (nearly one quarter), and 27 genera (nearly one quarter), but

[1] More critical figures compiled from the author's card register will be found in Tables I., II. and III. to follow.

include around 225 species (over one third of the total). The Octopoda, with only 8 families (one quarter) and 25 genera (slightly over one fifth), yet develop nearly 200 species (one third of the total). In comparison to this the single family and genus of Tetrabranchiata (3 generally recognized species) hold a minor place in the fauna.

The extraordinary development of the Œgopsida in families and genera is indicative, as the reader may anticipate, of the more than usual modification to which the different branches of this group have been subject, and we are to see that this is particularly true of the photogenic organs. The number of species on the other hand seems to have been held down by the circumstance that a very considerable proportion of the genera are pelagic types of widespread distribution, and, like so many other animals showing somewhat similar ecologic relations, do not break up well into species with our present degree of refinement in perception.

This brief survey of the classification may seem a digression, but without it as a guide, no consideration of the distribution of the photogenic function within the group as a whole or within its components could be entirely intelligible.

3. Distribution of the Photogenic Function among Cephalopods.

By no means all cephalopods are luminous. Among the entire major division of octopods but two species, *Melanoteuthis lucens* Joubin and *Eledonella alberti* Joubin, have been described as possessing photogenic organs, while even here the fact that the structures so described are actually designed for the production of light still remains to be demonstrated. The various instances where octopi have been observed to emit light are almost always poorly authenticated, though it is not impossible that in some cases, such as the observation by Darwin during the Voyage of the "Beagle," which will be noted later, are explicable on the assumption of infection by photogenic bacteria or protozoa. However that may be, and perhaps the point is not yet definitely settled, in the morphological evidence offered the two species mentioned stand quite alone.

On the other hand among the decapods photogenic properties are so widespread that taking the class as a whole, and even including the Octopoda, I am aware of no other major division of metazoan animals which shows such a proportional development of luminous species as the Cephalopoda.

It is therefore no wonder that the scattered literature, as well as the fragmentary character of the information to be gleaned therefrom, offers almost insurmountable difficulties to the inquiring student, while even reasonably complete information is scarcely to be found in any text-book or work of reference. There seems in fact no more recent effort on the part of teuthologists to meet this need than that of Chun (:10), which seems to have been carried out simply as an incident to the preparation of his monumental work on the "Valdivia" Œgopsids, an expensive and in the United States a relatively inaccessible volume. Furthermore he dealt with but one group of cephalopods, while even for this group there has now accumulated a considerable mass of additional information. In the English language by all odds the best and most trustworthy summary is the brief one of Hoyle (:08).

Probably the best way to convey an accurate idea of the manner of distribution of the photogenic function within the group is to present summarily a systematic survey of the entire class, carried down at least as far as genera, and including at the same time such appropriate supplementary data concerning the possession of this function as in each case is possible. An effort to do this is constituted in the following synopsis. In all cases an attempt is made to state as exactly as one writer can the number of valid or recognized species in each genus, and, in the case of photogenic forms, a full list of the species themselves, as well as an indication of the situation of their photophores. In a catalogue of this kind it must at the outset be admitted that the figures given are only approximate, due to the fact that entire elimination of the personal element is quite impossible, even though the concrete numbers quoted are not mere estimates, but represent in every instance an actual weighing of the validity of each specific name in the light of all available information, information which from the very nature of this paper cannot be gone into in any detail here. The attempt has been made to be both conservative and judicial, but it of course goes without saying that the result attained must be regarded as far from final. Aside from matters of judgment even, it would be presumptious to claim for this list either completeness or freedom from error, but every effort has been made to reduce unnecessary mistakes to a minimum, and after all it is utility rather than finality which must always be remembered as the end in view. In certain special cases where the number of valid species seems to be more than usually problematic, this circumstance has been so indicated by the use of + or ± signs.

Table I.[1]

SYNOPTIC TABLE OF THE CLASS CEPHALOPODA, SHOWING THE OCCURRENCE OF PHOTOGENETIC ORGANS.

Class **CEPHALOPODA.**

Order *TETRABRANCHIATA.*

Suborder NAUTILOIDEA.

Family *Nautilidæ.*
 Genus *Nautilus* Linnæus 1758. (No photogenic species known.)
  3 or 4 species.

Order *DIBRANCHIATA.*

Suborder DECAPODA.

Division ŒGOPSIDA.

Superfamily Architeuthoidea.

Family *Architeuthidæ.* (No photogenic species known.)
 Genus *Architeuthus* Steenstrup, 1857.
  14 species.

Superfamily Enoploteuthoidea.

Family *Gonatidæ.* (No photogenic species known.)
 Genus *Gonatus* Gray, 1849.
  3 species.

Family ONYCHOTEUTHIDÆ.
 Genus *Onykia* Lesueur, 1821. (No photogenic species known.)
  12 ± species.
 Genus ONYCHOTEUTHIS Lichtenstein, 1818. (2 axial photogenic organs in pallial chamber.)
  1 established species, *banksii;* several doubtful.
 Genus *Tetronychoteuthis* Pfeffer, 1900. (No photogenic species known.)
  2 species.
 Genus CHAUNOTEUTHIS Appellöf, 1891. (Photogenic organs in ventral integument of mantle—*Chun;* no luminous organs—Pfeffer.)
  1 species: *mollis.*

[1] Photogenic families and genera are printed in small capitals.

Genus *Ancistroteuthis* Gray, 1849. (No photogenic species known.)
1 species.
Genus *Moroteuthis* Verrill, 1881. (No photogenic species known.)
3 species.
Family LYCOTEUTHIDÆ.
Genus LYCOTEUTHIS Pfeffer, 1900. (Photogenic organs on eyes, in stalks of tentacles, and in pallial chamber.)
2 species: *diadema, jattai;* possibly identical.
Genus NEMATOLAMPAS Berry, 1913. (Photogenic organs on eyes, in arms, in stalks of tentacles, in pallial chamber, and at posterior tip of body.)
1 species: *regalis.*
Family LAMPADIOTEUTHIDÆ.
Genus LAMPADIOTEUTHIS Berry, 1916. (Photogenic organs on eyes, in stalks of tentacles, and in pallial chamber.)
1 species: *megaleia.*
Family ENOPLOTEUTHIDÆ.
Genus ENOPLOTEUTHIS d'Orbigny, 1844. (Photogenic organs on eyes and in the integument of mantle, funnel, head, and arms, but almost entirely confined to ventral aspect.)
3 species: *leptura, chunii, galaxias.*
Genus ABRALIA Gray, 1849. (Photogenic organs on eyes and in the integument of arms, head, funnel and mantle, but almost entirely confined to ventral aspect.)
7 species: *andamanica, armata, astrolineata, astrosticta, steindachneri, trigonura, veranyi.*
Genus ABRALIOPSIS Joubin, 1896. (Photogenic organs on eyes, at tips of ventral arms, and in the integument of arms, head, funnel, and mantle, but almost entirely confined to ventral aspect.)
5 + species: *affinis, hoylei, lineata, morisii, owenii, pfefferi.*
Genus WATASENIA Ishikawa, 1914. (Photogenic organs as in *Abraliopsis.*)
1 species: *scintillans.*
Genus ENOPLOION Pfeffer, 1912. (Larval form; photogenic organs on tentacle stalks and ventral integument of ventral arms, head, funnel, and mantle.)
1 species: *eustictum.*
Genus ASTHENOTEUTHION Pfeffer, 1912. (Larval form; photogenic organs on eyes.)
1 species: *planctonicum.*
Genus ANCISTROCHEIRUS Gray, 1849. (Photogenic organs in ventral integument of mantle.)
1 species: *lesueurii.*
Genus THELIDIOTEUTHIS Pfeffer, 1900. (Photogenic organs on tentacle stalks and ventral integument of head and mantle.)
1 recognized species: *alessandrinii.*
Genus PTERYGIOTEUTHIS H. Fischer, 1896. (Photogenic organs on eyes, in tentacle stalks, and in pallial chamber.)
4 ± species: *gemmata, giardi, hoylei, microlampas.*
Genus PYROTEUTHIS Hoyle, 1904. (Photogenic organs on eyes, in tentacle stalks, and in pallial chamber.)
3 species: *aurantiaca, margaritifera, oceanica,* + several named larval forms.

Family OCTOPODOTEUTHIDÆ.

Genus OCTOPODOTEUTHIS Rüppell, 1844. (Photogenic organs on ink sac?)

1 species: *sicula*.

Genus *Octopodoteuthopsis* Pfeffer, 1912. (No photogenic species known.)

1 species.

Genus *Cucioteuthis* Steenstrup, 1882. (No photogenic species known.)

1 species.

Family HISTIOTEUTHIDÆ.

Genus CALLITEUTHIS Verrill, 1880. (Numerous photogenic organs in integument of arms, head, and mantle; best developed ventrally.)

12 ± species: *asteroessa, chuni, dofleini, goodrichi, heteropsis, hoylei, japonica, meleagroteuthis, meneghini, miranda, ocellata, separata, verrilli*.

Genus HISTIOTEUTHIS d'Orbigny, 1839. (Photogenic organs as in *Calliteuthis*.)

1 species: *bonnellii*.

Genus HISTIOCHROMIUS Pfeffer, 1912. (Larval form; photogenic organs in integument of mantle on ventral aspect?)

1 species: *chuni*.

Family BENTHOTEUTHIDÆ.

Genus BENTHOTEUTHIS Verrill, 1885. (Photogenic o.gans on arms)

1 species: *megalops*.

Genus CTENOPTERYX Appellof, 1889. (Photogenic organs on eyes.)

1 species: *siculus*.

Superfamily Ommastrephoidea.

Family *Brachioteuthidæ*. (No photogenic species known.)

Genus *Brachioteuthis* Verrill, 1881. (+ *Tracheloteuthis* Steenstrup 1881.)

4 species.

Genus *Cirrobrachium* Hoyle, 1904(?)

1 species.

Family OMMASTREPHIDÆ.

Genus *Illex* Steenstrup, 1880. (No photogenic species known.)

2 species.

Genus *Todaropsis* Girard, 1889. (No photogenic species known.)

1 species.

Genus *Ommastrephes* d'Orbigny, 1835. (No photogenic species known.)

6 ± species.

Genus *Nototodarus* Pfeffer, 1912. (No photogenic species known.)

2 species.

Genus HYALOTEUTHIS Gray, 1849. (Photogenic organs in ventral integument of mantle.)

1 species: *pelagicus*.

Genus *Sthenoteuthis* Verrill, 1880. (No photogenic species known.)

4 species.

Genus *Symplectoteuthis* Pfeffer, 1900. (No photogenic species known.)

1 species.

Genus EUCLEOTEUTHIS Berry, 1916. (Bands of photogenic tissue on ventral aspect of head and mantle.)

1 species: *luminosa*.

Genus *Dosidicus* Steenstrup, 1857. (No photogenic species known.)

2 species.

Family *Thysanoteuthidæ.* (No photogenic species known.)

Genus *Thysanoteuthis* Troschel, 1857.

2 species.

(Position uncertain.)

Family *Lepidoteuthidæ.* (Naef refers this poorly known group to the Myopsida.)

Genus *Lepidoteuthis* Joubin, 1895. (No photogenic species known.)

1 species.

Superfamily Chiroteuthoidea.

Family *Chiroteuthidae.*

Genus *Doratopsis* de Rochebrune, 1884. (+ *Planctoteuthis* Pfeffer, 1912, and *Leptoteuthis* Verrill, 1884; no photogenic species known.)

7 species.

Genus Chiroteuthis d'Orbigny, 1839. (Photogenic organs on eyes, ventral arms, and in pallial chamber.)

7 species: *imperator, lacertosa, macrosoma, pellucida, picteti, regnardi* (photogenic organs undescribed), *veranyi.*

Genus Mastigoteuthis Verrill, 1881. (Photogenic organs in integument of the arms, funnel, mantle, or fins, or even absent.)

11 species: *dentata, famelica, levimana, magna.* (Not known to be photogenic.)

cordiformis (small tubercles, possibly photogenic, thickly distributed in dorsal integument of body).

agassizii (photogenic organs numerous in integument of head, arms, tentacle stalks and mantle, both dorsally and ventrally).

grimaldii (photogenic organs on dorsal surface of fins, and ventral surfaces of head, arms, funnel and mantle).

flammea (photogenic organs comparatively few; in integument of dorsal surface of fins, and on ventral surfaces of head, ventral arms, funnel and mantle).

talismani (photogenic organs on ventral aspect of fins).

hjorti (photogenic organs on eyes).

glaukopis (a photogenic organ in ventral border of each eyelid sinus).

Genus *Joubiniteuthis* nov.[1] (No photogenic species known.)

1 species.

Genus *Idioteuthis* Sasaki, 1916. (No photogenic species known.)

1 species.

Family *Grimalditeuthidæ.* (No photogenic species known.)

Genus *Grimalditeuthis* Joubin, 1898.

1 species.

Superfamily Cranchioidea.

Family Cranchiidæ.

Subfamily Cranchiinæ. (Series of small photogenic organs on eyes.)

Genus Cranchia Leach, 1817.

3 species or forms: *hispida, scabra, tenuitentaculata.*

Genus Liocranchia Pfeffer, 1884.

3 species or forms: *globulus, reinhardtii, valdiviæ.*

[1] *Chiroteuthis Portieri* Joubin, 1916, does not seem strictly referable to the genus in which it is placed, as it is said to possess no luminous organs, while the extreme attenuation and length of the three dorsal pairs of arms are at variance with the well known state of affairs in *Chiroteuthis.* Hence I would propose the new group *Joubiniteuthis,* with this species as type.

Genus Pyrogopsis de Rochebrune, 1884.
4 species: *pacificus, rhyncophorus, schneehageni, zygaena.*
Genus Leachia Lesueur, 1821.
3 species: *cyclura, ellipsoptera, eschscholtzii.*
Genus Liguriella Issel, 1908.
1 species: *podophthalma.*
Subfamily Taoniinæ. (A large single or duplex photogenic organ on each eyeball.)
Genus Phasmatopsis de Rochebrune, 1884. (Photogenic organs not yet described.)
1 species: *cymoctypus.*
Genus Toxeuma Chun, 1906.
1 species: *belone.*
Genus Taonius Steenstrup, 1861. (Photogenic organs not yet described.)
1 species: *pavo.*
Genus Verrilliteuthis Berry, 1916. (Photogenic organs not yet described.)
1 species: *hyperborea.*
Genus Megalocranchia Pfeffer, 1884.
5 species: *abyssicola, fisheri, maxima, pardus, pellucida.*
Genus Leucocranchia Joubin, 1912.
1 species: *pfefferi.*
Genus Taonidium Pfeffer, 1900. (Photogenic organs not yet described.)
4 species: *chuni, incertum, pfefferi, suhmi.*
Genus Crystalloteuthis Chun, 1906.
1 species: *glacialis.*
Genus Phasmatoteuthis Pfeffer, 1912.
1 species: *richardi.*
Genus Galiteuthis Joubin, 1898.
2 species: *armata, phyllura;* possibly identical.
Genus Corynomma Chun, 1906. (A pair of photogenic organs embedded in the liver in addition to the subocular photophores.)
1 species: *speculator.*
Genus Hensenioteuthis Pfeffer, 1900 (+ *Sandalops* Chun, 1906, *Helicocranchia* Massy, 1907, and *Teuthowenia* Chun, 1919.)
5 species: *antarctica, joubini, megalops, melancholicus, pfefferi.*
Genus Bathothauma Chun, 1906.
3 species: *bergeti, bouréei, lyromma.*

Division Myopsida.

Superfamily Loliginoidea.

Family *Loliginidæ.* (No photogenic species known.)
Genus *Acroteuthis* Berry, 1913.
3 species.
Genus *Doryteuthis* Naef, 1912.
5 species.
Genus *Loligo* Schneider, 1784.
32 ± species.
Genus *Lolliguncula* Steenstrup, 1881.
3 or 4 species.

Genus *Loliolus* Steenstrup, 1856.

4 species.

Genus *Sepioteuthis* de Blainville, 1824.

21 ± species.

Superfamily Spiruloidea.

Family SPIRULIDÆ. (A single organ thought to be photogenic at posterior end of body.)

Genus SPIRULA Lamarck, 1799.

11 named forms (number true species uncertain): *atlantica, australis, blakei, fragilis, indopacifica, laevis, peronii, prototypus, reticulata, spirula, vulgaris.*

Superfamily Sepioidea.

Family *Promachoteuthidæ.* (No photogenic species known.)

Genus *Promachoteuthis* Hoyle, 1885.

1 species.

Family *Idiosepiidæ.* (No photogenic species known.)

Genus *Idiosepius* Steenstrup, 1881.

2 species.

Family SEPIOLIDÆ.

Subfamily Rossiinæ. (No photogenic species known with certainty.[1])

Genus ROSSIA Owen, 1834.

14 species.

Genus *Semirossia* Steenstrup, 1887.

2 species.

Subfamily Heteroteuthinæ. (A fused pair of glandular photogenic organs on ink sac in all known cases.)

Genus HETEROTEUTHIS Gray, 1849.

3 species: *dispar, hawaiiensis, weberi.*

Genus STOLOTEUTHIS Verrill, 1881. (Photogenic organs still undescribed.)

1 species: *leucoptera.*

Genus IRIDOTEUTHIS Naef, 1912.

1 species: *iris.*

Genus NECTOTEUTHIS Verrill, 1883. (Photogenic organs still undescribed.)

1 species: *pourtalesii.*

Subfamily Sepiolinæ.

Genus SEPIOLA Schneider, 1784. (Paired glandular photogenic organs on ink sac.)

11 ± species: *affinis, atlantica, aurantiaca, intermedia*(?), *ligulata, pacifica* (?), *penares* (?), *robusta, rossiæformis* (?), *sepiola, steenstrupiana.*

Genus RONDELETIA Naef, 1916. (A fused pair of glandular photogenic organs on ink sac.)

1 species: *minor.*

Genus *Sepietta* Naef, 1912. (No photogenic species.)

4 or 5 species.

[6] This lack is stated by Naef (:12, p. 245) as one of the diagnostic characters of the subfamily, but the possession of photogenic organs by *Rossia macrosoma* is definitely affirmed by Meyer (:06, pp. 390, 392). One is perforce still of unsettled mind in the matter, especially as both observers worked at Naples, and Naef goes into no details beyond the mere negation.

Genus INIOTEUTHIS Verrill, 1881. (Paired glandular photogenic organs on ink sac.)

3 species: *japonica, maculosa, parva.*

Genus *Sepiolina* Naef, 1912. (No photogenic species known.)

1 species.

Genus EUPRYMNA Steenstrup, 1887. (Paired glandular photogenic organs on ink sac.)

8 ± species: *bursa, morsei, pusilla, schneehageni, scolopes, similis, stenodactyla, tasmanica.*

Subfamily Sepiadariinæ. (No photogenic species known.)

Genus *Sepiadarium* Steenstrup, 1881.

2 species.

Genus *Sepioloidea* d'Orbigny, 1855.

1 species.

Family *Sepiidæ.* (No photogenic species known.)

Genus *Sepia* Linnæus, 1758.

80 ± species.

Genus *Metasepia* Hoyle, 1885.

2 species.

Genus *Sepiella* Gray, 1849.

11 ± species.

Genus *Hemisepius* Steenstrup, 1875.

1 species.

Suborder OCTOPODA.

Superfamily Cirroteuthoidea.

Family CIRROTEUTHIDÆ.

Genus *Cirroteuthis* Eschricht, 1836. (No photogenic species known.)

8 species.

Genus *Stauroteuthis* Verrill, 1879. (No photogenic species known.)

3 species.

Genus MELANOTEUTHIS Joubin, 1912. (A pair of supposed photogenic organs on dorsal aspect of mantle.)

1 species: *lucens.*

Genus *Opisthoteuthis* Verrill, 1883. (No photogenic species known.)

6 species.

Genus *Cirrothauma* Chun, 1911. (No photogenic species known.[1])

1 species.

Genus *Froekenia* Hoyle, 1904. (No photogenic species known.)

1 species.

Genus *Vampyroteuthis* Chun, 1903. (No photogenic species known.)

2 species.[3]

Genus *Lætmoteuthis* Berry, 1913. (No photogenic species known.)

1 species.

Superfamily Argonautoidea.

Family *Ocythoidæ.* (No photogenic species known.)

Genus *Ocythoe* Rafinesque, 1814.

1 recognized species.

[1] A possibility seems to exist that this genus is photogenic,—cf. Chun, : 13, p. 23–25, 27.

[2] *Cirroteuthis macrope* Berry, 1911, appears to belong to this genus.

Family *Argonautidæ*. (No photogenic species known.)
Genus *Argonauta* Linnæus, 1758.
12 ± species.
Family *Tremoctopodidæ*. (No photogenic species known.[1])
Genus *Tremoctopus* delle Chiaje, 1829.
Only 1 certainly established species.
Family *Alloposidæ*. (No photogenic species known.)
Genus *Alloposus* Verrill, 1880.
2 species.

Superfamily Amphitretoidea.

Family *Amphitretidæ*. (No photogenic species known.)
Genus *Amphitretus* Hoyle, 1885.
1 species.

Superfamily Polypodoidea.

Family BOLITÆNIDÆ.
Genus *Bolitæna* Steenstrup, 1859. (No photogenic species known.)
1 species.
Genus ELEDONELLA Verrill, 1884.
5 species: (1 species, *alberti*, described as "probablement photogene").
Genus *Vitreledonella* Joubin, 1918. (No photogenic species known.)
1 species.
Family *Polypodidæ*. (No photogenic species known.)
Genus *Polypus* Schneider, 1784.
125 ± species.
Genus *Tritaxeopus* Owen, 1881.
1 species.
Genus *Pinnoctopus* d'Orbigny, 1845.
1 species.
Genus *Scæurgus* Troschel, 1857.
4 species.
Genus *Cistopus* Gray, 1849.
2 species.
Genus *Moschites* Schneider, 1784.
3 species.
Genus *Graneledone* Joubin, 1918.
9 species.
Genus *Eledonenta* de Rochebrune, 1884.
2 species.
Genus *Velodona* Chun, 1915.
1 species.

The increase afforded by the present list over the numbers included in the earlier catalogs of photogenic cephalopods is quite remarkable for the small number of years that has elapsed. Hoyle's list (:08, p. 14) records as photogenic 6 families, 26 genera, and 30 species of Œgopsida, 1 family, 3 genera and 3 species of Myopsida, and none of the other groups, or a total

[1] But cf. Tryon, '79, p. 131.

Table II.

RECAPITULATION OF RECENT CEPHALOPODA.

Class CEPHALOPODA.

Order TETRABRANCHIATA.

	Number of Genera.	Number of Species.	Number of Photogenic Species.
Suborder NAUTILOIDEA.			
Family *Nautilidæ*	1	3	0
	1	3	0

Order DIBRANCHIATA.

	Number of Genera.	Number of Species.	Number of Photogenic Species.
Suborder DECAPODA.			
Œgopsida.			
Family *Architeuthidæ*	1	14	0
Family *Gonatidæ*	1	2	0
Family ONYCHOTEUTHIDÆ	6	20±	2
Family LYCOTEUTHIDÆ	2	2	2
Family LAMPADIOTEUTHIDÆ	1	1	1
Family ENOPLOTEUTHIDÆ	10	27±	27
Family OCTOPODOTEUTHIDÆ	3	3	1?
Family HISTIOTEUTHIDÆ	3	14±	14
Family BENTHOTEUTHIDÆ	2	2	2
Family *Brachioteuthidæ*	2	5	0
Family OMMASTREPHIDÆ	9	20±	2
Family *Thysanoteuthidæ*	1	2	0
Family *Lepidoteuthidæ*	1	1	0
Family CHIROTEUTHIDÆ	5	28	14
Family *Grimalditeuthidæ*	1	1	0
Family CRANCHIIDÆ	18	41	34+
	66	173±	99+
Myopsida.			
Family *Loliginidæ*	6	72±	0
Family SPIRULIDÆ	1	1+	1+
Family *Promachoteuthidæ*	1	1	0
Family *Idiosepiidæ*	1	2	0
Family SEPIOLIDÆ	12	51±	26+
Family *Sepiadariinæ*	2	3	0
Family *Sepiidæ*	4	94±	0
	27	224±	27+
Suborder OCTOPODA.			
Family CIRROTEUTHIDÆ	8	23	1
Family *Ocythoidæ*	1	1	0
Family *Tremoctopodidæ*	1	1+	0
Family *Argonautidæ*	1	12±	0
Family *Alloposidæ*	1	2	0
Family *Amphitretidæ*	1	1	0
Family BOLITÆNIDÆ	3	7	1
Family *Polypodidæ*	9	148±	0
	25	195±	2

Table III.

SUMMARY.

	Familes.			Genera.			Species.		
	Total.	Photo-genic.	Per Cent. Photo-genic.	Total.	Photo-genic.	Per Cent. Photo-genic.	Total.	Photo-genic.	Per Cent. Photo-genic.
Œgopsida	16	10	62.5	66	39+	59.0	173±	99+	57.2
Myopsida	7	2	28.6	27	6+	22.2	224±	27+	11.6
Total Decapoda	23	12	52.2	93	45+	48.4	397±	126+	31.6
Octopoda	8	2	25.0	25	2	8.0	195±	2	1.0
Tetrabranchiata	1	0	0.0	1	0	0.0	3	0	0.0
Total	32	14	43.7	119	47+	39.5	595±	128+	21.3

of 7 families, 29 genera, and 33 species. Chun (:10, p. 39), treating only of the Œgopsida, increases these figures to 8 families, 26 genera and 39 species. The two sets of figures should be compared with those given in the numerical summary in Table III at the top of this page. Here it appears that of the 32 families of recent cephalopods now recognized, 14 (or more than two fifths) contain luminous species; out of 119 genera, 47 (or nearly two fifths) are light producing; and out of 595 species, 128 (or over one fifth) are now held on good ground to be luminous. The rich development in species of the genera *Loligo*, *Sepia* and *Polypus*, which has already been noted, is the circumstance chiefly responsible for the cutting down of the proportion which the luminous *species* bear to the whole to less than one half that which is exhibited by the luminous *families*. Similarly the slight proportional decline in the case of the luminous *genera* is due to the large number of ranking genera in certain mainly non-luminous families such as the Ommastrephidæ, Sepiolidæ, Cirroteuthidæ and Polypodidæ.

The table also indicates very strikingly what is really the outstanding feature of the taxonomic distribution of the photogenic forms, namely, the preponderance both of Œgopsida among the species known to be light producing, and of light producing species among the Œgopsida. In the former instance this preponderance is enormous. 71.4 per cent. of the luminous families, 83.0 per cent. of the luminous genera, 77.3 per cent. of the luminous species, are Œgopsid. Among the Œgopsida themselves over one half of all the families, genera, and species are described as possessing photogenic organs. Five entire families—the Lycoteuthidæ, Lampadioteuthidæ, Enoploteuthidæ, Histioteuthidæ, and Benthoteuthidæ, all of them of more or less deep sea habit,—have all their species so equipped, and this seems almost certainly true of the very aberrant but numerous Cranchiidæ as well. Among other groups of cephalopods, only the Spirulidæ can aspire to inclusion in the same category, and regarding them our information is still deficient. There may be only one valid species in this family. In addition to those named, one other œgopsid family (Chiroteuthidæ) has more than half its species light producing. On the other hand luminous species for five œgopsid families (the Architeuthidæ, Gonatidæ, Thysanoteuthidæ, Lepidoteuthidæ and Grimalditeuthidæ), five of the seven myopsid families, six of the eight octopod families, and the Nautilidæ, are as yet unknown.

For multiplicity and variety of luminous forms the palm must be awarded to the Enoploteuthidæ and Cranchiidæ, though, as will subsequently appear, the maximum attainment and diversity of structure of the photogenic organs themselves is reached not in either of these families, but in the Lycoteuthidæ.

4. Actual Observance of the Phenomenon.

As compared with other Mollusca, or even with other general groups of Invertebrata, Cephalopoda, and especially those of the decapod section, are extremely difficult either to capture, to maintain alive under artificial conditions, or even to observe with any degree of satisfaction in their free condition. Among the Œgopsida it is probable that a sheer majority of the genera have never been seen at all in the living state, at any rate by any human eyes but those of fishermen. It is therefore not to be wondered at that actual observance of the phenomenon of light production in this group of animals is an extremely rare event, possible only occasionally or under very exceptional conditions. The published records of such observations are consequently so scattered that they have fallen into obscurity, or else, in the case of some of the more spectacular ones become all the more conspicuous by very reason of their paucity and desultory character.

A brief historical survey of this subject has been given by Hoyle (:08), but the most valuable contributions thereto have been made since that time, while Hoyle himself omitted one or two quite interesting accounts from his summary. It will therefore be well to review briefly the entire field.

I have been no more successful than previous authors in the discovery of any recorded observation of photogenic phenomena in living Cephalopoda prior to that of Vérany in the case of *Histioteuthis bonnellii* (*bonelliana*), ('51, p. 119), a translation of which is quoted in full by Hoyle in the paper cited and is well worthy of repetition here.[1]

"As often as other engagements permitted, I watched the fishing carried on by the dredge on the shingly beaches which extend from the town of Nice to the mouth of the Var. On the afternoon of September 7, 1834, I arrived at the beach when the dredge had just been drawn in, and saw in the hands of a child a cuttle-fish, unfortunately greatly damaged. I was so struck by the singularity of its form and the brilliance of its color that I at once secured it, and, showing it to the fishermen, asked whether they were acquainted with it. Upon their replying in the negative I called their special attention to it, and offered a handsome reward for the next specimen secured, either alive or in good condition, and then passed on to other fishermen and repeated my promise. Shortly afterwards I was summoned and shown a specimen clinging to the net, which I seized and placed in a vessel of water. At that moment I enjoyed the astonishing spectacle of the brilliant spots, which appeared upon the skin of this animal, whose remarkable form had already impressed me: sometimes it was a ray of sapphire blue which blinded me; sometimes of opalescent topaz yellow, which rendered it still more striking; at other times these two rich colors mingled their magnificent rays. During the night these opalescent spots emitted a phosphorescent brilliance which rendered this mollusc

[1] Vérany's monograph is a very rare one in the United States, especially in the West, where I am not aware that any complete copy exists. I am accordingly entirely dependent for the information quoted upon the translation given by Hoyle.

one of the most splendid of Nature's products. Its existence was, however, of short duration, though I had placed it in a large vessel of water. Probably it lives at great depths."

Although not mentioned by Hoyle, the next student whose published observations concern us was none other than Charles Darwin. Among the melange of odd notes in the course of his account of the voyage of the "Beagle" ('60, pp. 7–8) appears the following: "I was much interested, on several occasions, by watching the habits of an Octopus, or cuttle-fish. . . . I observed that one which I kept in the cabin was slightly phosphorescent in the dark." As we have already seen, photogenic organs or tissues are practically unknown among octopods, so that this observation would be quite an anomalous and puzzling one, were it not for the at least plausible explanation that the phenomenon in this instance as so many others in the literature of biophotogenesis was due not to the active functioning of any tissues of the cephalopod itself, but to bacterial infection or even to the presence of effulgent Protozoa in the slime surrounding its skin. Another possibility which occurs to me is that the animal may not have been examined in absolute darkness, but that sufficient light penetrated into the chamber, though imperceptible to the unadjusted human eye, to enable the iridocytes in the skin of the octopus to yield a pseudo-luminous reflection, analogous to that so notorious in the case of the eyes of many mammals. The description by Giglioli of luminescent specimens of a squid which he identified as "*Loligo sagittatus*" and certain Chilean octopods, referred to by Holder in the quotation given in the next paragraph, may be susceptible of similar explanation. To the original of this work with the description of his observations I have unfortunately not been able to gain access. For my own part I have on several occasions attempted to discover similar properties in captive specimens of the common southern California devilfish, *Polypus bimaculatus* (Verrill), but so far with only negative results. Final settlement of the question can only be accomplished by careful experiment.[1]

[1] Since this paragraph was put in type I am reminded that Tryon ('79, p. 131) in his paraphrase of the description of *Tremoctopus gracilis* (Souleyet 1852) says that this species is "phosphorescent and with metallic reflections when living." I have been unable to check this observation by reference to the original work of Souleyet.

In a popular volume by C. F. Holder ('87, p. 46), descriptive of luminous organisms in general, but unfortunately none too carefully compiled, occurs the following paragraph on the Cephalopoda:

"The highest forms of the *Mollusca*, the Cephalopods, cuttle-fishes, are probably at times luminous. I have noticed what I presumed was a delicate, sensitive glow about an *Octopus* in a semi-darkened tank, but I am not satisfied to make the statement as a fact. These forms are so remarkable for the waves of color that pass over them, and which seem to make them transparent, that one could readily be deceived.

"The little *Cranchia* (Plate IV., Fig. 2) is a light-giver, its phosphorescence having been distinctly observed. It is an ally of the giant squids, which have been found fifty-five feet in length, and which, if luminous like their pygmy relative, would present a marvelous spectacle, darting veritable living arrows through the depths of the sea.

"Giglioli refers to the phosphorescence of *Loligo sagittatus*, and to that of several small Octopods observed by him at Callao and Valparaiso. Their bodies gave out a pale whitish light, uniformly distributed."

It happens that *Cranchia* is a genus which is now known to possess definite photogenic organs, but these have been found to occur only on the eyeball, whereas the rather poor figure given by Holder represents the animal as brightly and evenly glowing over the entire surface,—body, head, arms, tentacles, and all. As to the supposed photogenic properties of *Polypus* and related octopods,—both Darwin and Giglioli would seem to have been too accurate observers for the explanation advanced by Holder to be entirely satisfactory.

Chun, in his narrative of the cruise of the "Valdivia" (:03, pp. 569–570; also :03*a*, p. 81; :10, p. 50) gives up to this time the fullest account of the actual display of photogenic propensity by a cephalopod we have been able to find, and he followed this in later publications by a very considerable contribution to our morphological knowledge of the organs responsible for the manifestation. The specimen observed proved to belong to a wonderful undescribed species, the *Lycoteuthis diadema* (Chun).

Although it was taken from a considerable depth, he was able to keep it alive in ice water long enough to make a photograph of it by dint of its own light. Again I must quote from a translation by Hoyle: "Among all the marvels of coloration which the animals of the deep sea exhibited to us, nothing can be even distantly compared with the hues of these organs. One would think that the body was adorned with a diadem of brilliant gems. The middle organs of the eyes shone with ultramarine blue, the lateral ones with a pearly sheen. Those towards the front of the lower surface of the body gave out a ruby-red light, while those behind were snow-white or pearly, except the median one, which was sky-blue. It was indeed a glorious spectacle." It is altogether a pity that similar observations have not been possible for the doubtless even more spectacular *Nematolampas regalis*, which, although very nearly related to *Lycoteuthis* is equipped with an entire further battery of photophores.

More detailed from the standpoint of physiology is the account given by Watasé (:05) of a little squid, the "hotaru-ika" of Japanese writers,[1] which is extremely abundant at the proper season and locality on certain of the shores of Japan, and which has since become the best known of all the luminous squids. Watasé's paper is an important one as the first dealing with this species, but, being semi-popular in character and published in Japanese, escaped notice for a considerable time and has only lately received a little of the attention it deserves. Through the kindness of Mr. Sotaro Matsushita, formerly of Redlands, California, I have for some time been in possession of a translation, and a very free transcription of some of its more interesting if quaint passages should be neither inappropriate nor unwelcome here. "Hotaru-ika, when seen externally, does not differ much from other *ika* [squids]. Yet there are many interesting features which we do not see in other *ika*. At each end of the two 'legs' there are three oblong, black spots. These small spots were first discovered by the French scientist Joubin. Yet even he did not know their function. According to the results of my own study of these in living Japanese specimens, the spots were found to produce a considerable light, penetrating to the space of about

[1] The "firefly squid"—*Watasenia scintillans* (Berry).

a foot. . . . While the animal is living these spots are transparent.

"Again there are hundreds of other small spots all over the body. . . . When seen in daylight they appear to be small black spots, but in the night all these spots shine with a brilliant light like that of the stars in heaven. . . . When these spots (while the *hotaru-ika* is alive) are viewed under the microscope, they are very interesting. When the animal is about to produce the light, the membranes [chromatophores] covering the spots will concentrate and remove themselves, thus opening a way for the light. The light is so brilliant that it seems like a sunbeam shot through a tiny hole in a window curtain. Again when the *hotaru-ika* wishes to shut off the light, the membranes will expand and cover the spots. . . ."

In the following year Meyer (:06) described briefly the photogenic activity of the myopsid, *Heteroteuthis dispar* (Rüppell), similar observations having been made some time previously by Lo Bianco, but never published. Meyer found that in the case of the specimen observed by him at the Naples Zoölogical Station he "could in the dark room easily locate the position of the photophore through the transparent mantle, lying on the ventral surface just behind the anus." He further found that when the animal was irritated, "it shot rapidly through the water, and spurted through its funnel a luminous secretion which floated in the water as separate globules, these being drawn out by the currents into shining threads, a pyrotechnic display (*Feuerwerk*) which he was able to repeat many times. The light of the secretion and of the light organ itself had the same pale greenish hue which we observe with our glow-worms." Meyer further reports the discovery by one of his colleagues, Marchand, of somewhat similar photogenic properties in *Sepiola*, except that in this genus "the luminous secretion is not discharged into the water but remains on the surface of the gland. Furthermore, *Sepiola* only shines if it be very powerfully stimulated, as when, for instance, the mantle is cut open." From the foregoing it is at once evident that in both these myopsid genera the mechanism of light production is very different from that of any of the other forms studied, and this conclusion is borne out by the anatomical features. The possible utility of this peculiar development of the function, so far as *Heteroteuthis* is concerned, is the subject of some interesting speculation in one of Meyer's subsequent papers (:08, pp. 507–508), which will receive more attention later on.

We are now brought to a consideration of some important recent work performed by various Japanese observers in continuation of Watasés pioneer studies on *Watasenia scintillans* (Sasaki, :12, :13, :14; Ishikawa, :13). This constitutes probably the chief work which has been done in this field, and therefore merits consideration in considerable detail.

"In the region where the squids live, that is, in the waters of Namerikawa on the coast of the Japan Sea," writes Ishikawa (:13, pp. 167–169), "this circumstance [the luminosity of the tips of the ventral arms described by Watasé] had already long been known; but none of our zoölogists were aware of it until Watasé by chance made the discovery. At a time when he was engaged in the study of fireflies, he was apprised by a schoolmaster that there occurred a species of squid in the sea at Namerikawa which lighted very strongly. Pursuant to this suggestion he sought the village named, found in due course a species of small squid with powerful light organs, and recognized the same as a species of *Abraliopsis*. As he has orally told me, it was on the 28th of May, 1905, on the memorable day of the battle of Tsusima, hat he saw the light of this squid for the first time. . . . . .

"The large swellings at the tips of the ventral arms, as well as two or three smaller dots, are, as he remarks, luminous organs of the first order. They shine so brilliantly that when one observes the animals in dark water, one sees only two effulgent bodies moving in the dark water, like the glow of an electric contact, and the lively oscillations of the invisible arms produce a very wierd effect. Next to these in the intensity of their light are the eye organs, and then come the remaining organs. The three types of organs do not always shine simultaneously; often only one or the other. But it can also happen that the animal sets all the organs into action at the same time. When the mantle organs light up, the form of the animal springs out spectre-like in the dark water. These organs, arranged in rows, when one examines them close at hand, shine like an electric illumination. The color of the light is a beautiful clear blue.

"As Watasé writes, the arm organs in dead animals are entirely surrounded by pigment cloaks and only when alive can the animal retract these. The retraction of these cloaks takes place very quickly, and when they are retracted, the organ appears in daylight as a delicate dull-green colored body."

In a paper which comprises a most notable contribution to our knowledge of the ecology and habits of ten-armed cephalopods, Sasaki (:14, pp. 77–80) adds materially to the accounts of his predecessors. Some of his observations are so pertinent to some of the discussion which must follow later that they should be quoted rather fully. Treating the three types of photophore to be seen in *Watasenia* under separate headings, this author writes:

"*Brachial Organ.* This is the largest organ, and when I made observations in the fishing season, it was much more active in phosphorescence than other organs. It is situated at the end of each ventral arm, composed of 3 globules arranged in a series. The globules are ovoid in shape and nearly equal in size, but the middle one in the series is generally a little larger than the others, the dimensions being 1.4 mm. long and about 1 mm. broad. In fresh specimens they show a greenish cobalt colour, and there are 2 or 3 layers of large brownish chromatophores covering a part of the preceding substance. These chromatophores are constantly contracting and expanding. When they were observed at night on the living animals, they were seen to discharge light in all directions much brighter than any of Japanese fireflies. The color of the light is Prussian-blue or tinged a little with purple, and the luminosity is strong enough to outshine the other luminous organs. When the living animal was placed on a glass plate, which was put directly on the case of the dry plate of the photographic camera, and then exposed for four seconds with the Lion's dry plate of the special rapid no. 230, the light of this brachial organ was distinctly taken on the dry plate, although those of other organs made no impression.

"*Minute Organs Scattered on the Ventral Surface of the Whole Body.* There are numerous minute organs distributed on the ventral surface of the mantle, head and siphon, and they are also on the third and fourth arms. . . .

"Each organ in the fresh specimen has a substance of purplish hue in the centre; this substance seems to be that discharging light when the animal is living. When the organ is exposed in the air, the purplish hue of the substance changes to greenish blue after a while, and finally resolves into a true green. The substance is covered by a pigment layer of darkish brown or deep purple which has a hole resembling the pupil of an eye, through which the substance can easily be seen. The light of the substance at night is whiter and less luminous than that of the brachial organ.

"*Ocular Organ.* When the eyelid of the fresh specimen is removed and the eyeball exposed, there are seen 5 luminous organs arranged in a series along the ventral circumference of the eyeball, the organ on either end of the series being a little larger than the remaining 3. The colour of all these organs is pearly white. When the organ is seen at night in the living animal, the phosphorescence is not distinguishable from that of the minute organ on the body.[1]

"*Difference of Phosphorescence in the Sexes.* On examining the preserved specimens to discover the difference of the external forms as well as the histological structures of their luminous organs as occurring in the male and female, none could be discerned. But in the female specimens there are one hundred or so more of the minute organs of the mantle than in the male. Whether there is any meaning as to sexual selection, it is difficult to say, the data concerned being insufficient at present to announce any opinion.

"Next, as to the difference of phosphorescence between the sexes in their living state, the means of investigation proved to be very difficult. At first I repeatedly undertook to keep the animal in an aquarium, but no success was attained. The reason for the failure is that first of all, the animals are very delicate, and next the aquarium was defective. The animals

[1] A slight discrepancy is noteworthy between the account of Sasaki and that of Ishikawa concerning the character of the light of the subocular organs. According to the latter these photophores are more or less intermediate in brilliancy between the large brachial organs and those of the general integument.

are so weak that in carrying them from the sea to the aquarium they wasted and died. As they wasted, the luminosity in question became very feeble, and naturally with their expiration, the light of the luminous organs gradually vanished altogether. This being so, I then tried to observe the animals directly while they were swimming in the net. But no good means were found easily to distinguish the sexes on such dark nights, even with the feeble light of the moon or of a lantern.

"However in my examinations at night, no special variety of the light could be found, the colour of the light being always the same. And in one case, putting in a vessel and observing about thirty specimens in a fishing boat while they were yet actively on motion, I verified the fact that their luminosity is uniform. In the morning, to my surprise, a male was found dead among those 30 specimens; this proves that it had the same colour of light with the female on that night. The above data seem to prove the fact that the colour of the light of the luminous organs is the same in both sexes.

"Again, in late July of the same year, I made another observation on the phosphorescence under consideration and then it was quite evident to me that the luminosity of the brachial organ was at this season noticeably feebler than in the spring.

"The phosphorescence of the immature animal can never be studied in Namerikawa, young ones thus far not being found there."

In the same paper (pp. 98–99), Sasaki incidentally records the fact that he observed the photogenic property in living specimens of the myopsid, *Inioteuthis japonica* Verrill (= *inioteuthis* (Naef)). These he found to be "discharging a faint cobaltish light from a great luminous organ which is situated in the mantle cavity near the ink-bag." From anatomical observations we know that the luminous organs of this genus are essentially similar to those of the nearly related if not actually congeneric *Sepiola.*

Lastly, Dahlgren (:16, pp. 70–71) describes in a little greater detail than before the photogenic behavior of *Heteroteuthis dispar*, the myopsid species already observed by Meyer. He writes: "When brought into the laboratory in good condition and allowed to rest quietly it may be taken into the dark-room and gently struck, as it swims in the aquarium, with a glass rod. Fig. 18 is a drawing to illustrate what may and usually does happen under these circumstances. The animal throws out of its siphon several little masses of mucus which show no light at the moment of ejection, but almost instantly, as the oxygen of the water begins to work on them, show a number of rod-shaped particles of a brilliantly luminous matter embedded throughout the very delicate mass. As the mass continues to expand this light continues to glow brightly for as much as three to five minutes, after which it rather suddenly dies out. In color the light is the usual blue-green of luciferine when burning outside the body. The animal can repeat this process for a number of times, when it appears to have exhausted its supply of luciferine, and it is not possible, apparently, to keep it in captivity for a long enough period for the supply to be restored."

From this scanty, but for all practical purposes probably exhaustive summary, we find that except for the doubtful observations by Souleyet, Darwin and Giglioli, the actual process of light production in cephalopods has been observed directly in but seven species, of which three belong to the myopsid family Sepiolidæ and have photogenic organs of a peculiar discharging type, while the other four belong to the Œgopsida. We are fortunate, however, in that each of these latter species is representative of a different family and thus ample support is given to the inferences necessarily drawn from the outward appearance and histological structure of the many types of photophore that they are of a fact photogenic.

(*To be Continued*)