

THE BRITISH ASSOCIATION.

SECTION D.

ZOOLOGY.

OPENING ADDRESS BY WILLIAM E. HOYLE, M.A., D.Sc.,
PRESIDENT OF THE SECTION.

(Abridged.)

THE impression left upon my mind by a score of Presidential Addresses to this Section, which it has been my privilege to hear, is that the speaker who treats of the subject matter of his own researches has the best prospect of making his remarks interesting and profitable to his audience. It is, therefore, in no spirit of egotism that I invite your attention this morning to the small and economically unimportant group of the Cephalopoda.

Some of my predecessors have been men who walked, so to speak, on the heights; who undertook the culture, or at all events the surveillance, of large domains. The extensive views and broad principles which they have thus been able to lay before the Section have been such as at once to compel the attention of all who are interested in any department of biology, or indeed of any branch of science at all. My own case has been far different; the plot I have tried to cultivate has been a very small one, and I have had but little leisure to peep over the fence and see what my neighbours were doing. I come before you, therefore, as a specialist, and not only so, but as that most humble kind of specialist—a systematist (a "mere systematist" is, I believe, the common phrase)—one whose main work has been the discrimination and definition of genera and species. I feel that some apology is necessary in asking zoologists of all departments to step for an hour into my particular allotment and see what has been going on there during the last few decades.

Before inviting you to enter, however, I should like to plead that even the systematist has his uses; for, properly considered, what is the systematic arrangement of any group of animals but the condensed formal expression of our present knowledge regarding its morphology, ontogeny, and phylogeny? Furthermore, how could the varied and complex problems of geographical distribution be attacked without the materials prepared by the systematist?

Having said this much by way of apology and defence, let me invite you without further prelude to consider two or three questions suggested by the study of the Cephalopoda.

Just half a century ago (August 1, 1857), there appeared in the *Annals and Magazine of Natural History* the translation of a paper by the late Prof. Steenstrup, of Copenhagen, which has ever since been regarded as marking an epoch in our knowledge of the Cephalopoda. The consideration of the scope and significance of this memoir may profitably engage our attention for a short time. In researches which were then comparatively recent, Vérany and Vogt and Heinrich Müller had shown that, in the genera *Tremoctopus* and *Argonauta*, the hectocotylus, a supposed parasitic worm which had been found in the mantle-cavity of the female, was in reality one of the arms of the male which had become detached and found its way thither, bearing with it the fertilising element—a procedure quite unique, not only among the Cephalopoda, but also among the Mollusca, if not in the whole animal kingdom. The gist of Steenstrup's discovery was that, although the separation of an arm was peculiar to very few forms, the modification of one or other of the arms for reproductive purposes was of common occurrence among the Cephalopoda; and, furthermore, that the situation of the particular arm, which was so modified, varied with the systematic position of the genus in question, and was constant through the main divisions of the class. To this less extensive modification of the arm he gave the name "hectocotylisation."

Stimulated by this discovery, other zoologists examined the Cephalopoda in their possession, and described the modifications in various genera, and now it is universally recognised that no definition of the Cephalopod is complete which does not include a description of the position and form of the hectocotylised arm. The descriptive anatomy

of this organ is fairly well known. Out of twenty-two families, which may be regarded as well established, its structure is known in a number of genera in no fewer than twelve, whilst of the remaining ten it has been more or less conclusively shown that in seven no modification of the arm takes place, so that there are only three families in which we are still without any information regarding it.

Our knowledge of the physiology of the apparatus has not, however, advanced with anything like the same rapidity. Even in the case of those forms where a true hectocotylus is found (*Argonauta*, *Tremoctopus*, and *Ocythoe*) it is not known for certain whether the fertilising arm is deposited by the male in the mantle-cavity of the female (as I think is most probable), or whether (as is stated by some writers) the arm breaks off when mature and finds its own way to its destination. This much is certain, that for some time after its detachment it possesses the power of independent movement.

As regards the function of the modified but not detachable arm, we have the important and interesting observations of Racovitza made at Roscoff and Banyuls on the genera *Polyopus* (*Octopus*) and *Sepiolo*. It appears that in the first of these forms the extremity of the hectocotylised arm of the male is introduced into the mantle-cavity of the female, both individuals resting on the sea-bottom and at some distance from each other (about 25 cm. in the case of a male measuring 1.25 m. in total length). Although after an encounter the female appeared to flee the embraces of the male, and although the males, when two were placed in the same tank, fought with each other, there was no sign of any combat between the sexes as was described by Kollmann. In *Sepiolo* the female is roughly seized by the male, and held with the ventral surface uppermost; the two dorsal arms are introduced into the mantle-cavity, whilst the other three pairs hold the female firmly. The efforts of the male are directed to keeping the female from attaching herself to any firm support. It would appear that the introduction of the arms of the male into the mantle-cavity interferes with the respiration of the female, and that she makes desperate efforts to escape as soon as she can attach herself to any neighbouring object. In this respect there is a marked contrast between the behaviour of these two genera, and it is greatly to be desired that observations should be made on other forms, but the difficulties in the way of this have hitherto proved insuperable.

Although, as we have seen, but little is known of the actual working of the hectocotylised arm, there are differences in the structures set apart in the female for the reception of the spermatophores, which correspond with the different arrangements of the hectocotylus in the male. For example, in *Polyopus* (*Octopus*) the spermatophores are deposited in the termination of the oviduct; in *Rossia* there is a large plicated area surrounding the mouth of the oviduct for their reception; whilst in the nearly related *Sepiolo* there is a pouch-like depression of the integument lying beside the mouth of the oviduct for the same purpose (von Maehrenthal). In *Sepia*, *Loligo*, and the other Myopsids in which the ventral arms are hectocotylised the spermatophores are received upon a specially modified area lying just to the ventral side of the mouth.

From this all too brief sketch of the function of these organs we may now return to the question of the systematic value of the modified arm of the male. Prof. Steenstrup was firmly convinced of the paramount importance of the hectocotylisation as a classificatory character, and he seemed to cling to this belief almost with the ardour of a devotee for a religious principle. In 1881 he published a memoir in which a new classification of the genera *Sepia*, *Loligo*, *Rossia*, and some other forms was propounded, based avowedly on the position of the hectocotylised arm; and when this scheme was attacked by the late Dr. Brock of Göttingen, he defended it vigorously in a further communication, placing at its head the following thesis, much in the same spirit as Luther nailed his famous theses to the church door at Wittenberg: "Hectocotylatio bene observata et rite considerata divisionibus naturae semper congruit; incongrua divisionibus, eas arbitrarias et factitias esse indicat."

Steenstrup further explains that the point of most conse-

quence is which pair of arms is affected by the hectocotylistation, whether the first, third, or fourth pair; next in importance comes the nature of the modification; while the question whether the right or left arm is affected is quite insignificant. It will be our business to consider how far the Danish naturalist's position is justified in the light of our present knowledge.

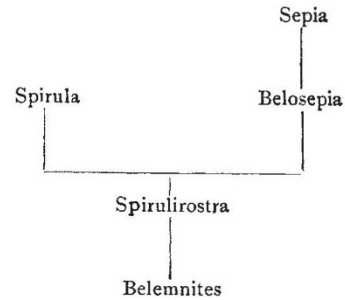
An inspection of the facts known up to the present time shows, first of all, that where hectocotylistation is known to take place it affects either the first, third, or fourth pair of arms; no instance is yet known where the second pair is modified, except in subsidiary relation to another pair, or in one or two rather doubtful cases in which all the arms are said to be modified. It appears, furthermore, that hectocotylistation of the third pair is confined to the Octopoda, while the first and fourth pairs are affected in the Decapoda, so that, as far as the main divisions of the Dibranchiata are concerned, the position of the hectocotylus is a correct index to them. We may, however, go a step further still, and point out that in every family, with one exception, the position of the hectocotylistated arm is constant within the limits of the family, so that there is a very strong *prima facie* case for the truth of Professor Steenstrup's dictum. The difficulty arises when we come to consider the family Sepiolidae and its allies, and endeavour to form an idea of their relationships to each other.

Steenstrup was so convinced of the truth of his thesis that he divided the Myopsida into two main divisions according to whether hectocotylistation affected the first or fourth pair of arms, and placed the four genera *Sepiadarium*, *Sepioloidea*, and *Idiosepius* (notwithstanding their *Sepiola*-like form) with *Spirula*, apart from *Sepiola* and *Rossia*, and along with *Sepia* and *Loligo*. It becomes necessary now to inquire how far this classification is justified by what we know of the morphology of the forms concerned.

It will be convenient to deal in the first place with *Spirula*, which has always been of great interest on account of the unique structure and position of its shell. It still belongs to the greatest of zoological varieties, only a dozen specimens with the soft parts having been obtained, of which one alone proved to be a male. This was examined by Sir Richard Owen, who described the hectocotylistation as affecting both the ventral arms, which are much enlarged, exceeding the others both in length and thickness: they are quadrangular in section, devoid of suckers, and the right is much larger than the left. The other arms appear to have a round truncated extremity which may be a secondary modification. The relationships of *Spirula* have recently been made the subject of inquiry by Prof. Paul Pelseneer, who completed the memoir in the *Challenger* reports begun by Prof. Huxley, and by Dr. Einar Lönnberg of Stockholm, who dissected a specimen obtained for him from Madeira by the late Captain Eckman. These two investigators arrived at different conclusions regarding its systematic position.

Pelseneer regards it as an *Cegopsid*, Lönnberg as a *Myopsid*, but the anatomical characters on which they are agreed are enough to show that, at any rate, these two forms cannot be so closely related to each other as to belong to the same sub-family, or even family.

With regard to the question at issue between them as to the *Cegopsid* or *Myopsid* nature of *Spirula*, I think, on the whole, that its resemblance is to the former rather than to the latter; but I believe that the branch of the ancestral tree which terminates in *Spirula* was given off from the main Cephalopod stem before the *Cegopsida* and *Myopsida*, as we now know them, had been separately evolved. Palæontology reveals a possible descent of *Spirula* from a Belemnitoid through such an intermediate form as *Spirulirostra*; and from this, on the other hand, it is easy to conceive of the descent of *Sepia* through a form resembling *Belosepia*. Such a relation could be expressed by the following diagram, which is, however, only a rough illustration of possibilities, for *Spirulirostra* is a Miocene form and *Belosepia* an Eocene, so that the former could hardly be the ancestor of the latter. It is only contended that these forms indicate a possible line of descent.



Unfortunately, in the present state of our knowledge, it is impossible to correlate the above diagram with one based upon the study of the soft parts of recent forms. It is sufficient if they do not contradict each other. We know nothing of the soft parts of the fossils, and there is no recent form, which exhibits shell characters, bridging over the gulf between *Sepia* and *Spirula*. To sum up, *Spirula* must be regarded as, at all events, the representative of a distinct family: it is not unlikely that it may one day become the type of a division coequal with *Myopsida* and *Cegopsida*, and it does not appear to me that the structure of its hectocotylistated arms would be any argument against such a view.

We may now consider the genera *Idiosepius*, *Sepiadarium*, and *Sepioloidea*, regarding which there can be no doubt that on morphological grounds these three genera are more nearly allied to the *Sepiolidae* than to the *Sepiidae* or *Loliginidae*; in fact, practically the only character of any importance which points in the opposite direction is the hectocotylistation. This portion of the subject has been very fully and clearly handled by Dr. Appellöf of Bergen, and to his memoir I refer those who desire more detailed information. We have here, then, a case in which forms the ventral arms of which are hectocotylistated are more nearly related to forms with dorsal hectocotylistation than to others with ventral, and this shows that the position of the modified arm (or arms) is not by itself an infallible guide to systematic affinity. It is a striking instance of an aphorism of the late Prof. Rolleston, that "no single character can be regarded as a safe basis for a natural classification until it has been proved to be so."

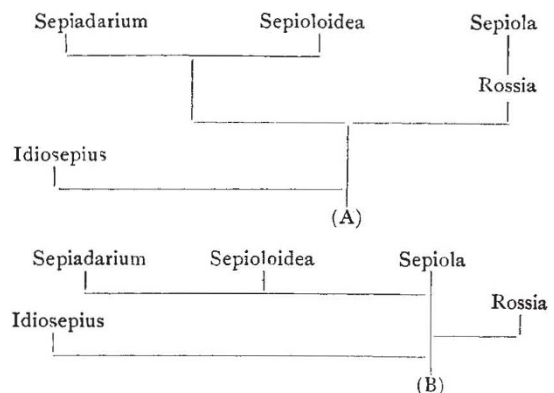
It may, however, be worth while to look a little further into the relationships of these forms, and to see whether the hectocotylistation of the dorsal arms is quite as sporadic and irregular as it at first appears.

After the separation of *Idiosepius* two possibilities present themselves as to the further evolution of this group.

A. The main stem divided into two branches leading to *Rossia* and *Sepiola* on the one hand, and to *Sepiadarium* and *Sepioloidea* on the other.

B. The stem gave off first a branch leading to *Rossia*, and subsequently divided into two, one leading to *Sepiola* and the other to *Sepiadarium* and *Sepioloidea*.

These two alternatives may be expressed graphically thus:



These schemes are not entirely satisfactory. Certain difficulties are common to them both. The posterior salivary glands, which, it is assumed, were inherited in a fused condition from the primitive *Ægopsid* stem, and remain in that condition in *Rossia*, have been separated in *Idiosepius*, *Sepiadarium*, and *Sepiolo*, as well as in *Sepia* and *Loligo*.

Furthermore, A presents the difficulty that the fusion of the mantle with the head in the nuchal region has been acquired independently by *Idiosepius*, *Sepiadarium*, and *Sepioloidea*; and *Sepiolo*.

On the other hand, B has the disadvantage of assuming that the hectocotylisation has been transferred from the fourth to the first pair of arms independently in *Rossia* and *Sepiolo*.

If, as I believe to be the case, scheme A is admitted to offer the lesser of the two difficulties, it has the advantage of indicating that the hectocotylisation of the ventral arms has been directly inherited from the main stem common to *Myopsids* and *Ægopsids*, and has only been transferred to the dorsal arms in the branch common to *Rossia* and *Sepiolo*.

Hence we reach the conclusion that, although the variations in the structure and position of the hectocotylus follow pretty closely the systematic divisions of the Dibranchiata, we are not justified in maintaining that the position of the hectocotylised arm is by itself a sufficient guide to the systematic position of a doubtful form; it is only one of many characters that must be taken into consideration.

The subject of fossil Cephalopoda has not formed any part of my own special researches, but a contribution has recently been made to our knowledge of these forms to which it seems desirable to allude, because it deals, not with systematic or stratigraphical facts, but with conclusions which may be drawn from shell structure as to the life-history and habits of certain important and interesting forms. Prof. Jaekel, formerly of Berlin, now of Greifswald, the author of the memoir referred to, lays down a number of theses regarding the organisation and mode of life of these extinct species, and I venture to give an abstract of his views, premising that my acquaintance with palæontology does not justify me in expressing a definite opinion as to the validity of his conclusions, though they seem extremely reasonable.

His opening statement is that *Orthoceras* and its allies were not free-swimming but sessile organisms, and this is based on the following arguments amongst others. The shells were thicker and heavier than any that are found in pelagic organisms; the external sculpture shows that the shell was not embedded in the soft parts, and if it were exposed the annulate arrangement of many forms is inconsistent with their easy passage through the water; the "lines" (in the naval architect's sense of the word) of an organism intended for navigation are always smooth and not wavy; otherwise undue friction against the water would be created; whilst the straight transverse margin of the aperture of the shell shows that it was not carried by a creeping body like that of a snail. Their sessile nature is further shown in the first place by the radial symmetry, which is rare in free-swimming forms, and almost unknown in those the axis of which is long in proportion to their diameter. Further, the termination of the shell is generally broken off: of all the thousands of specimens which have been examined, but very few show the initial chamber; in those cases in which the apex is preserved it shows a scar, where the siphuncle entered the protoconch. The separation of the shell into chambers by transverse septa occurs only in sessile forms, but in such it is found in many divisions of the animal kingdom. The reason of this cameration is to be found in a constant effort to keep the body of the animal above the surface of the mud in which it is rooted. On this view the siphuncle admits of a simple explanation; it is the vestigial part of the body which has been contracted and partially cut off as the body has moved successively forward to the enlarged superior portion of the shell.

It may be added that J. M. Clarke has recorded a case in the American Upper Devonian rocks in which the

majority of the large *Orthoceratidæ* were fossilised in a vertical or but slightly sloping position.

The forms such as *Phragmoceras*, &c., in which the aperture of the shell is contracted, and often shows bilaterally symmetrical notches, are interpreted as having lived buried in the mud. The notches served for the protrusion of the arms, vent, and siphon, which latter were probably elongated tubes stretching up through apertures excavated in the mud, much in the same way as the heart-urchin (*Echinocardium*) among the sea-urchins lives buried in the mud, and obtains nourishment by stretching its tube feet up to its surface. The arrangement of the arms was probably like that seen in the embryos of Dibranchiata, or of the circumoral appendages of *Nautilus*.

Turning to the extensive and interesting group of *Belemnites*, Prof. Jaekel enunciates the view that these were not, as has been commonly believed, active free-swimming forms, the rostrum (guard) serving as the pointed ram of a battleship, but stationary, the rostrum playing the part of a pile by which they were rooted in the mud at the sea-bottom, like the pointed base of a *Flabellum* or other deep-sea coral, or the anchor-spicules of a glass-ropes sponge. In favour of this view may be adduced the size, weight, and solidity of the rostrum, which, if the animal moved about in a horizontal attitude, would have thrown its centre of gravity too far towards that end of the body: its circular section, which points to a radial, not a bilateral, symmetry, and hence, as above mentioned, to a sessile rather than a free-swimming habit. The pointed form of the rostrum would be admirably adapted to fixation in a muddy bottom, whilst its weight would render it a very effective anchor. Further, it is to be noted that *Belemnites* are found abundantly in strata of argillaceous origin.

This view has a strong recommendation in the fact that it presupposes gradual progress in the Cephalopoda in the direction of greater mobility as evolution advanced, thus:

- A. *Orthoceras*—firmly attached.
- B. *Belemnites*—anchored in the mud.
- C. Recent Dibranchiata—free-swimming.

Another interesting discovery of Prof. Jaekel is that of a slab of Solenhofen stone, upon which are certain specially arranged impressions, apparently made by the hooks on the arms of a Cephalopod. If this determination is correct, the fact is of the greatest interest, for it would show that these animals walked upon the ground with the head downwards and the distal extremity of the body elevated; that in them the arms were not merely morphologically, but also functionally, the equivalent of a foot.

In conclusion let me direct your attention to a subject which is almost entirely the growth of the last fifteen years. I mean the discovery and investigation of luminous organs in the Cephalopoda. These have now been observed in no fewer than twenty-nine out of about seventy well-characterised genera of Decapoda, and have been found to present a most interesting variety in position and in structure.

Before passing on, however, to consider the structure of these organs, it may be well to lay before you the evidence on the strength of which a photogenic function has been ascribed to them. The actual observations are remarkable chiefly for their paucity; indeed, it may seem to some that the foundation of solid fact is too slender for the superstructure raised upon it, but still due consideration will show that this is not the case. The first recorded occurrence of phosphorescence in the Cephalopoda is due to Vérany, and dates back rather more than seventy years, though it was not published till 1851. The description is so definite and concise as to be well worth quoting:

"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 colour 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 colours mingled their magnificent rays. During the night these opalescent spots emitted a phosphorescent brilliance which rendered this mollusc 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."

The species thus referred to was *Histioteuthis bonelliana*, which we shall have occasion to refer to in the sequel.

The next observation, so far as I am aware, was made by Prof. Chun, on board the *Valdivia* during the German deep-sea expedition, on a form which he has called *Thaumtolampas diadema*. The specimen captured lived long enough to allow of a photograph being made of it whilst in a state of functional activity, and the appearance it presented is thus described by the observer:

"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."

Finally we have the genera *Heteroteuthis* and *Sepiolo*, the phosphorescent properties of which were seen last year by Dr. W. T. Meyer and Dr. W. Marchand in the Zoological Station at Naples.

This short list comprises all the actual observations on the luminosity of these animals; in these, however, the photogenic function has been definitely associated with special organs, and it is by comparison with these that other organs in other species have been regarded as having the same significance.

The history of the anatomical examination of these organs dates back only to the early 'nineties, and, so far as I can ascertain, the right of priority of the discovery rests with Prof. Joubin, who made a communication to the Société scientifique et médicale de l'Ouest at Rennes on February 3, 1893, a brief account of which was published by the Société de Biologie of Paris on the 10th of the same month: this communication related to *Histioteuthis rüppelli*, and in it attention was called to Vérany's observation quoted above. Sections of the organs of *Abraliopsis* were exhibited at the Göttingen meeting of the German Zoological Society and at the Nottingham meeting of this Association in the same year. Successive memoirs by Joubin and others followed, and in 1903 Prof. Chun delivered an address to the German Zoological Society at Würzburg, in which he gave a masterly survey of the whole subject, brought forward instances of similar organs previously overlooked, and showed the great variety in structure, not only in the organs of different species, but even in organs of one and the same individual.

More or less adequately authenticated luminous organs have now been recorded in no fewer than thirty-three species of Cephalopoda, and they have been found to occur in the following situations:

- (1) Ventral surface of mantle.
- (2) Ventral surface of body-wall within the mantle-cavity.
- (3) Ventral surface of siphon.
- (4) Ventral surface of head.
- (5) Ventral surface of arms (usually confined to the ventral and ventro-lateral, rarely found on the dorso-lateral, and very rarely on the dorsal).

- (6) Ventral surface of eyeball.
- (7) Ventral surface of tentacles.
- (8) Dorsal aspect of the dorsal arms.
- (9) Dorsal surface of fin.

The most striking fact apparent from this summary is that luminous organs are practically confined to the ventral aspect of the animal. Another remarkable fact is the existence of organs concealed beneath the mantle and beneath the integument covering the eyeball, which can only be effective by reason of the transparency of the tissues in the living creature.

To give a detailed description of the structure of these many and varied organs would be out of place on the present occasion; it must suffice to group them into more or less well-defined classes and take an example from each.

The luminous organs of Cephalopoda may be divided in the first instance into

- A. Glandular.
- B. Non-glandular.

A. Glandular Organs.—In this class we have to deal only with the type of structure found in *Heteroteuthis*, *Sepiolo*, and *Rossia*, which has been investigated by Dr. W. T. Meyer, of Hamburg, a pupil of Prof. Chun. When working at the Naples Zoological Station he was fortunate enough to obtain a specimen of *Heteroteuthis dispar*, and Dr. Lo Bianco called his attention to its luminous properties. On examination in a dark room it was easy to see the organ lying on the ventral surface of the body, just behind the funnel, showing through the transparent mantle with a pale greenish light like that of the glowworm. It appeared, further, that when the animal was irritated it shot rapidly through the water, leaving behind it a trail of luminous secretion which floated in the form of separate globules, and were afterwards drawn out by the currents into long threads. Dr. Meyer was able to repeat this exhibition of fireworks several times.

In *Sepiolo* the luminous secretion is not ejected, but remains attached to the surface of the gland; and, furthermore, the light is only given off on powerful stimulation, as, for example, when the mantle is cut open. The structure of these organs has as yet been only very briefly described by their discoverer: they consist of paired glands, situated as above described one on either side of the anus, and partially concealed by the lateral margin of the ink-sac, which forms a recess for their reception. Beneath and to the inner side of the gland there is a reflector, and above it is a rounded gelatinous mass, fibrous in structure, transparent during life, covered with a delicate muscular layer. Dr. Meyer hesitates as to the function of this mass; but I think, in view of the structure of the luminous organs in other species, we may hazard the suggestion that it is some kind of lens. This organ is of particular interest, because it is the only instance yet recorded of a luminous organ among the Myopsida and the only glandular luminous organ in the Cephalopoda. Glandular luminous organs are, however, known in many species of fish, and in *Pholas* among the Mollusca.

B. Non-glandular Organs.—These may perhaps be divided into

- (i.) Simple, without special optical apparatus.
- (ii.) Complex, with more or fewer of the following structures: pigment layer, reflector, lens, diaphragm.

(i.) As a type of the simpler kind we may take the branchial organ of *Pterygioteuthis giardi*, in which we have a central mass of parenchymatous tissue, with a delicate superficial membrane (consisting of two thin layers), and resting upon a rather thick layer of close, compact tissue, which stains very deeply; beneath this organ is a single layer of cells containing a reddish-brown pigment. The corresponding organ in the nearly allied *Pyroteuthis* (or *Pterygioteuthis*) *margaritifera* is a degree more complex, for underneath the central cell mass is a thick layer of scale-like bodies, similar in structure to that regarded in other cases as a reflector ("tapetum" of Chun). In both these cases it seems necessary to regard the central cells as the source of light (see Fig. A).

Another organ, almost equally simple, is that found in the tentacles of *Thaumtolampas*, where the central por-

tion of the stem of the tentacle for about 2 mm. of its length is occupied by a large rounded cell-mass whose diameter is more than half that of the tentacle. The nerve which usually occupies this position is pushed to one side and flattened out like a ribband. Most curious is the fact that on the side opposite to the nerve a second organ is superposed on the first, which is of more complex structure, inasmuch as it has in its centre a mass of photogenic cells surrounded by a system of radiating fibrils with a pigment layer and tapetum at one side (see Fig. 1).

(ii.) As an example of the complex organs we may conveniently take those of *Histioteuthis rüppelli*, where they are scattered over the ventral surface of the mantle, siphon, head, and arms, forming in particular a definite ring round the ventral half of the margin of the ocular aperture. The organ itself is an ovoid body, about 1 mm. in length and somewhat less in diameter. The deeper three-fourths of this cup are covered with a thin layer of pigment, which is lined with a thick coating made up of small lenticular bodies packed closely together and forming a kind of mirror. The space within this, equal in diameter

phores. The photogenic cells lie rather in front of the centre, and before them again a ring of black cells seems to discharge the functions of an iris diaphragm. Behind the source of light is a reflector consisting of two parts: the deeper is concave, spheroidal, and made up of numerous concentric layers; the more superficial portion is conical, and also composed of concentric lamellæ. Partly in front of and partly behind the diaphragm is a lenticular mass of tissue. These little lanterns are scattered in considerable numbers over the ventral surface of the mantle, funnel, head, and arms, and the appearance of the animal when they are functionally active must be brilliant in the extreme (see Fig. c).

If we examine the organs just described and the others above enumerated, we see that certain conditions are fulfilled in all cases—namely, the presence of a mass of deeply staining, active cells with distinct nuclei, supplied with blood-vessels and nerves. These, then, are the essential parts of the apparatus, though even here differences obtain: for example, in *Thaumatolampas* the cells are polyhedral, highly refractile, and clearly defined, with spherical nuclei and distinct nucleoli. In *Chiroteuthopsis* the cells are few and large, and partially fuse one with another. In *Pterygioteuthis* the fusion has proceeded so far that the cell-boundaries are no longer recognisable, and there is present a finely granular mass in which numerous nuclei of varying size may be distinguished. In other cases the cells branch out into fibres and form a reticulate structure (*Calliteuthis*). In rare cases, as, for instance, the tentacular organ of *Thaumatolampas*, above described, this essential part constitutes the whole organ; but generally other structures are superadded, such as a pigment coat, reflector ("tapetum" of Chun), lens, and diaphragm, as has been mentioned in the complex organs just described.

Numerous interesting questions at once suggest themselves in regard to these structures, and it is very disappointing to admit that in regard to almost every one the answer is a confession of ignorance. The first inquiry is: What is the origin of these organs, and from what primitive structures are they evolved? Here it is possible to say but little; there is no instance in which the development of these organs in the embryo has as yet been studied. A larva, believed to be that of *Histioteuthis*, came into my hands a short time ago, and full of hope I had a portion of the mantle cut into sections, but with no result whatever; there was nothing which I could interpret as the rudiment of such an organ.

Those organs occur in so many and such scattered families that it seems clear they must be polyphyletic. Furthermore, even in one and the same species the different organs are not all constructed on the same plan. In *Abrialiopsis*, for example, the pallial organs are quite different from the ocular; but the most striking example of this sort of complexity is found in the remarkable *Thaumatolampas*, which has altogether twenty-two organs constructed on no fewer than ten different principles. It seems difficult in such a case to resist the conclusion that these organs have been separately evolved at different times, and perhaps from different origins, during the phylogenetic history of the species.

This variety in the structure of these organs naturally suggests the query: Do these differently designed lamps give out different kinds of lights? Here we have the observation of Prof. Chun on board the *Valdivia* to guide us, according to which in the living animal the middle

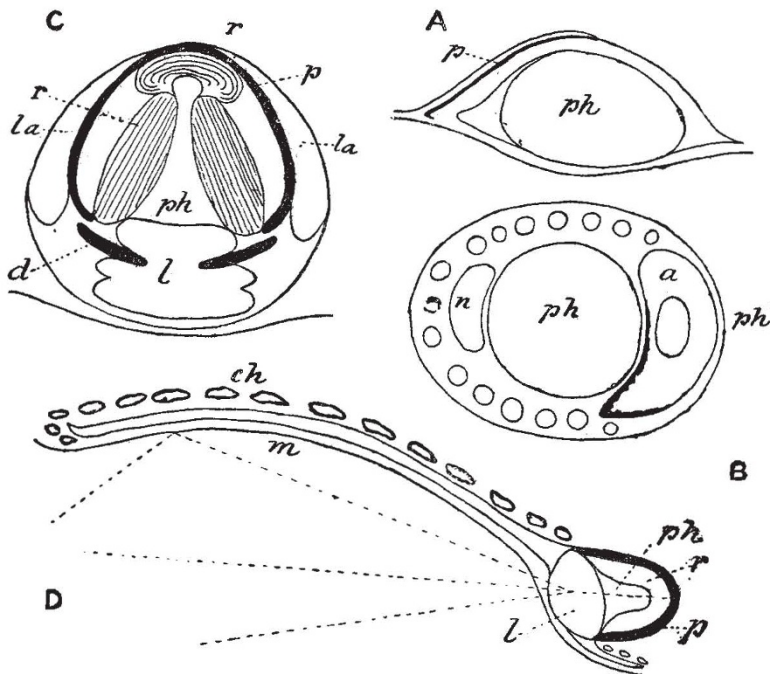


FIG. 1.—Semi-diagrammatic sections of typical luminous organs:—A, Branchial organs of *Pterygioteuthis giardi*. B, Tentacular organs of *Thaumatolampas*. C, Pallial organ of *Abrialiopsis*. D, Pallial organ of *Histioteuthis rüppelli*. a, Accessory tentacular organ. ch, Chromatophores. d, Diaphragm. l, Lens. la, Lacuna. m, Mirror (external). n, Nerve. p, Pigment. ph, Photogenic cells. ph', Photogenic cells of accessory organ. r, Reflector (internal).

to about half the diameter of the organ, is filled with a mass of large deeply staining cells with large distinct nuclei. The more superficial portion of the organ is made up of what seem to be refractive structures. The deeper portion is conical, fitting into a hollow in the photogenic mass, whilst the upper part is bounded by a definite convex surface, the function of which is obviously lenticular. Nerves have been traced passing through the mirror to the light-producing cells in the centre. This ovoid body is situated at the posterior end of a somewhat hollowed patch of an elongated oval shape, which may measure as much as 10–12 mm. in its antero-posterior diameter. A consideration of the form and position of this hollowed patch and of its relation to the axis of the organ shows pretty clearly that it is an external mirror, destined to throw the rays of light downwards and forwards (see Fig. D).

One of the most complicated organs known is that found in the mantle of *Abrialiopsis*. Here the whole apparatus is spheroidal in form and surrounded by a black coating, derived apparently from a number of confluent chromato-

nothing which I could interpret as the rudiment of such an organ.

Those organs occur in so many and such scattered families that it seems clear they must be polyphyletic. Furthermore, even in one and the same species the different organs are not all constructed on the same plan. In *Abrialiopsis*, for example, the pallial organs are quite different from the ocular; but the most striking example of this sort of complexity is found in the remarkable *Thaumatolampas*, which has altogether twenty-two organs constructed on no fewer than ten different principles. It seems difficult in such a case to resist the conclusion that these organs have been separately evolved at different times, and perhaps from different origins, during the phylogenetic history of the species.

This variety in the structure of these organs naturally suggests the query: Do these differently designed lamps give out different kinds of lights? Here we have the observation of Prof. Chun on board the *Valdivia* to guide us, according to which in the living animal the middle

ocular organ shines with an ultramarine light, whilst the middle of the five ventral organs is sky-blue and the anal organs are ruby-red. It may also be observed that even in preserved specimens, when examined in a strong light, the different organs seem to shine with different colours, although there is under such conditions no actual emission of light. Furthermore, in some forms (e.g., *Calliteuthis*) there are chromatophores in the superficial layers of the integument over the luminous organs, through which the light admitted must pass. A somewhat similar arrangement obtains in the curious structures in *Chiroteuthis*, which were regarded by Joubin at the time of their discovery as "thermoscopic eyes," but which are, I think rightly, in the present state of our knowledge, considered to be a special kind of luminous organ. In these instances the function of the superficial chromatophores may be to colour the light which passes through them.

The question of the utility of these variously coloured lights to the creature possessing them admits of an answer which is, at all events, extremely plausible. It was suggested in the case of deep-sea fishes by Brauer, and has been adopted by Chun in reference to the Cephalopoda. They serve as recognition marks by which the various species can identify their fellows; just as certain colour patches in the plumage of birds enable them to find their mates, so in the darkness of the ocean abysses do these fairy lamps serve their possessors. Another and perhaps even more obvious utility is suggested by the general distribution of these organs. It has above been pointed out that they are, almost without exception, on the ventral aspect of the body, that is, the inferior surface in the position in which the animal habitually swims. It must happen, therefore, that when the creature is moving over the floor of the ocean in the quest for food, this must be illuminated by its lamps, and the advantage of a series of searchlights playing over the ground will be at once apparent.

Finally we have the question: How is the light produced? To this we can only say that this is an instance of the transformation of one kind of energy into another. We are quite familiar with the production of heat in the animal body by the processes of oxidation which go on in it; we are also familiar with the production of kinetic energy when a muscle contracts under a nervous stimulus; and we are also aware that electric discharges are produced under similar conditions in certain organs of the Torpedo and other fish. The production of light is a phenomenon of the same kind. When we can explain how stimulation applied to a nerve causes contraction in a muscle, then, and not till then (so far as I can see), shall we be within reasonable distance of explaining the action of these living lamps.

One point is worthy of notice which has been ascertained, not by experiments on the Cephalopoda, but on other animals, namely, the remarkable economy of this illuminant. A perfectly infinitesimal proportion of the energy expended is wasted on the production of heat. From this point of view animal phosphorescence puts to shame our most modern devices. Whether we shall ever be able to rival Nature in this respect remains to be seen.

We have thus shown how rapid has been the growth of our knowledge regarding the distribution and structure of these fascinating organs, and yet how little we have learned of the mode of their operation, and we end, as all scientific inquiries end when pursued far enough, with a confession of ignorance.

What I have ventured to lay before you are a few of the fruits of the little garden plot in whose culture I have been privileged to take a humble share. If it has appeared to you that the labour spent upon their production by a few enthusiastic workers has been well expended; if they show that in this, as in any other group of animals, the study of small details conscientiously carried out leads to problems of the deepest interest, my object in the preparation of this Address will have been fully achieved.

NO. 1974, VOL. 76]

MATHEMATICS AND PHYSICS AT THE BRITISH ASSOCIATION.

ON Thursday, August 1, at 10 a.m. Prof. A. E. H. Love, F.R.S., read his presidential address, which has already appeared in full in these columns (see NATURE, August 1). A vote of thanks, moved by Sir D. Gill and seconded by Sir G. Darwin, was carried with acclamation.

The Hon. R. J. Strutt commenced the ordinary proceedings with a paper on helium and radio-activity in common ores and minerals. He was inclined to attribute the helium which can be obtained from minerals, not to a radio-activity of the rocks themselves, but to the radium which they contain. The evidence on which this conclusion was based is that the ratio of radium to helium present is nearly constant. A great exception occurs in the case of beryl, which shows no radio-activity, but contains a large quantity of helium. Prof. Rutherford suggested that thorium should be looked for in beryl as a source of the discrepancy. In his reply, Mr. Strutt stated that he had found thorium in granite but not in beryl in sufficient quantities to afford an explanation of its peculiar behaviour.

Lord Kelvin followed with a paper on the motions of ether produced by collisions of atoms or molecules containing or not containing electrions. To him it seems extremely improbable that differences of grouping atoms all equal and similar should suffice to explain all the different chemical and other properties of the great number of substances now commonly called chemical elements. The impossibility of the transmutation of one element into any other he declared to be almost absolutely certain. The ether he takes as an elastic, compressible, non-gravitational solid. It is, however, only under the enormous forces of attraction or repulsion exerted by atoms on ether that augmentation or diminution of its density is practically influential. Purely dynamical reasoning leads him to infer generally similar theorems for an atom to those worked out by Heaviside for an electron. The association of atoms with electrions (or atoms of resinous electricity), and the interaction of both with the ether, form the basis of a general explanation of physical phenomena.

In a paper on secular stability, Prof. Lamb explained the difference between ordinary or temporary stability, i.e. stability as asserted by the method of small oscillations, and secular stability, i.e. stability when account is held of possible frictional forces; and he gave an experimental illustration of the latter kind. A pendulum hangs by a Hooke's joint from the lower end of a vertical shaft which can be made to rotate by a pulley with constant angular velocity ω . The effect of the rotation is that its two circular component vibrations have different periods, that one being the faster the direction of revolution of which agrees with that of the shaft. The criterion of secular stability imposes a limit to the speed for which the vertical position of the shaft is stable; for speeds higher than the limiting one a new position of equilibrium is possible in which the pendulum rotates at a constant inclination θ given by $\cos \theta = Mgh / (A - C)\omega^2$, where A and C are the two principal moments of inertia of the pendulum at the joint.

The beginning of the session on Friday had been allotted to a discussion on the constitution of the atom, and the committee of the section had not been in error in expecting that this would be of intense interest. Prof. Rutherford, whom we now have permanently in this country, opened it with a speech which was specially intended to suggest lines for discussion rather than to be a dogmatic statement of his own views. It was perfectly clear, however, that he regarded the electron as having come to stay, although at present it is impossible to decide whether the electrons which are set free in radio-activity or are revealed by the optical properties of an atom are merely an outer circle or are a revelation of the internal constitution of the inner core of the atom. He declared in favour of a kinetic view of the atom in opposition to statical views such as that developed by Lord Kelvin. Only on a kinetic theory could the great velocity of the β particles be explained. Sir O. Lodge in his contribu-