ON THE ORIGIN AND METAMORPHOSES OF INSECTS*

IV.

On the Nature of Metamorphoses

IN the preceding articles we have considered the life history of insects after they have quitted the egg. It is obvious, however, that to treat the subject in a satisfactory manner we must take the development as a whole, from the commencement of the changes in the egg, up to the maturity of the animal, and not suffer ourselves to be confused by the fact that all insects do not leave the egg

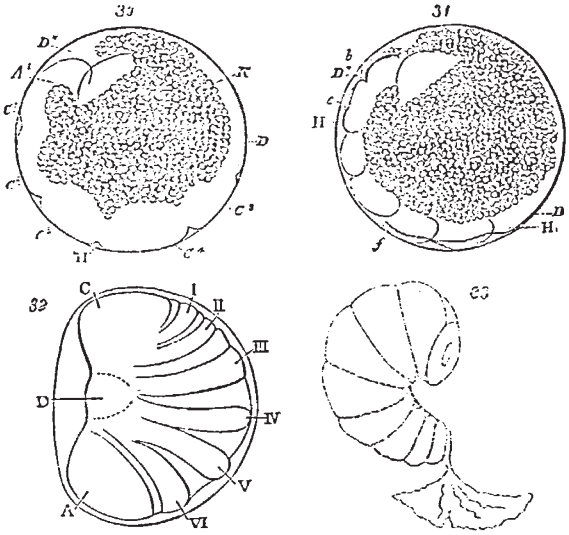

FIG. 30.—Egg of Phryganea (Mystacides). A^1, mandibular segment; C^1 to C^3, maxillary, labial, and three thoracic segments; D, abdomen. (after Zaddach). 31, Egg of Phryganea somewhat more advanced. *b*, mandibles; *c*, maxillæ; *c f s*, rudiments of the three pairs of legs. 32. Egg of Pholcus opilionides (after Claparede). 33, Embryo of Julus after Newport).

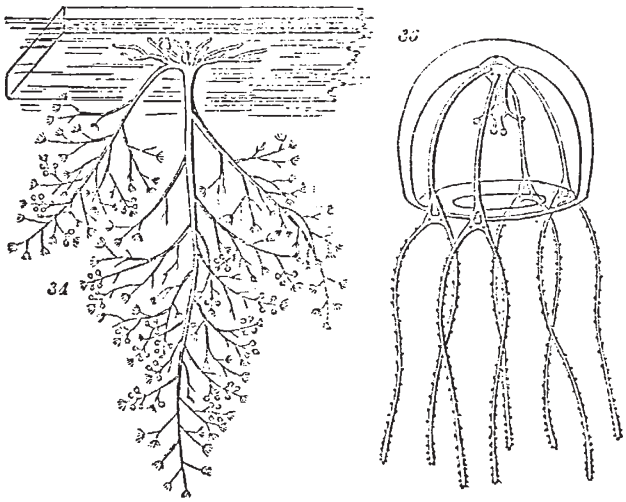

FIG. 34.—Colony of Bougainvillea fruticosa, natural size, attached to the underside of a piece of floating timber (after Allman). 36, The medusa from the same species.

in the same stage of embryonal development. For although all young insects when they quit the egg are termed "larvæ," whatever their form may be (the case of the so-called Pupipara not constituting a true exception), still it must be remembered that some of these larvæ are much more advanced than others. It is evident that the larva of a fly, as regards its stage of development, corresponds in reality neither with that of a moth nor with that of a grasshopper. In fact, insects quit the egg in very different stages. The maggots of flies, in which the appendages of the head are rudimentary, belong to a lower grade than the grubs of bees, &c., which have antennæ, mandibles, maxilla, labrum, labium, and, in fact, all the mouth parts of a perfect insect. The caterpillars of Lepidoptera are generally classed with the vermiform larvæ of Diptera and Hymenoptera, and placed in opposition to those of Orthoptera, Hemiptera, &c. But, in truth, the possession of thoracic legs places them, as well as the similar larvæ of the Tenthredinidæ, on a decidedly higher level, while in the development of the cephalic appendages there is, as already mentioned, a marked difference between the maggots of flies and the grubs of bees. Thus, then, the period of growth (that in which the animal eats and increases in size) occupies sometimes one stage in the development, sometimes another; sometimes, as for instance in the case of *Chloeon*, it continues through more than one, or, in other words, growth is accompanied by development. But, in fact, the question is even more complicated than this. It is not only that the larvæ of insects at their birth offer the most various grades of development, from the grub of a fly to the young of a grasshopper or a cricket; if we were to classify larvæ according to their development, we should have to deal not with a simple case of gradations only, but with a series of gradations, which would be different according to the organ which we took as our test.

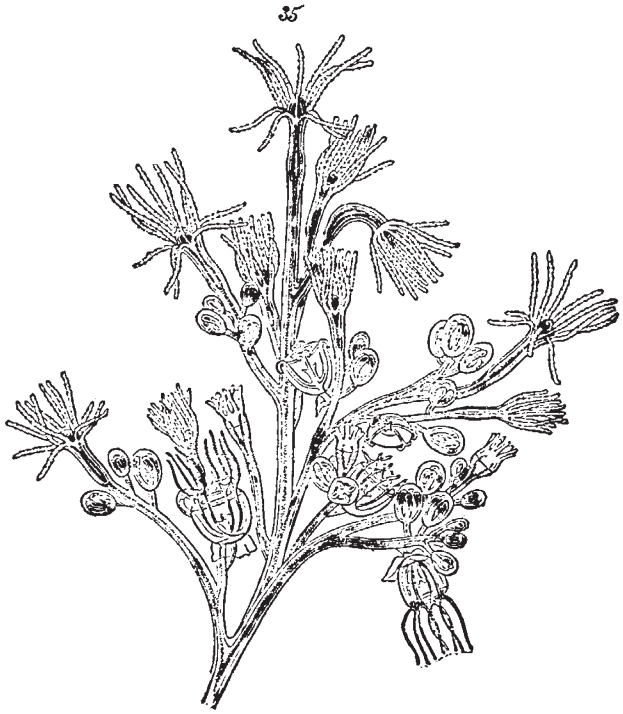

FIG. 35.—Portion of Colony of Bougainvillea fruticosa, more magnified.

Apart, however, from the adaptive changes to which special reference was made in a previous article, the differences are those of gradation, not of direction. The development of a grasshopper does not pursue a different course from that of a bee or wasp, but the embryo attains a higher state before quitting the egg in the former than in the latter; while in most Hymenoptera the body-walls and internal organs are formed before the thoracic appendages; in the Orthoptera, on the contrary, the legs

* Continued from p. 31.

make their appearance before the body-walls have completely closed round the yolk.

Prof. Owen,* indeed, goes so far as to say that the Orthoptera and other Homomorphous insects are, "at one stage of their development, apodal and acephalous larvæ, like the maggot of the fly; but, instead of quitting the egg in this stage, they are quickly transformed into another, in which the head and rudimental thoracic feet are developed to the degree which characterises the hexapod larvæ of the *Carabi* and *Petalocera*."

I quite believe that this was originally true of such larvæ, but from the tendency which large and important organs have, to appear at an early stage of embryonal development, the fact now appears to be, so far at least as can be judged from the observations yet recorded, that the legs of those larvæ which commence life with these appendages, generally make their appearance before the body-walls have closed, or the internal organs have approached to completion. Indeed when the legs first appear they are merely short projections, which it is not always easy to distinguish from the segments themselves. It must, however, be admitted, that the observations are neither so numerous, nor in most cases so full, as could be wished.

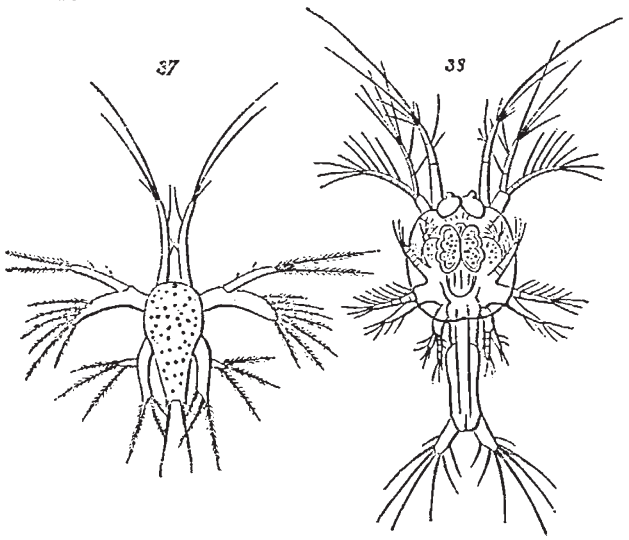

FIG. 37.—Larva of Prawn, Nauplius stage (after F. Muller). 38, Larva of Prawn, more advanced, Zoea stage.

Fig. 30, for instance, represents an egg of Phryganea, as represented by Zaddach in his excellent memoir,† just before the appearance of the appendages. It will be seen that a great part of the yolk is still undifferentiated, that the side walls are incomplete, the back quite open, and the segments only indicated by undulations. This stage is rapidly passed through, and Zaddach only once met with an egg in this condition; in every other specimen which had indications of segments, the rudiments of the legs had also made their appearance, as in Fig. 31, which, however, as will be seen, does not in other respects show much advance on Fig. 30.

Again in Aphis, the embryology of which has been so well worked out by Huxley,‡ the case is very similar, although the legs are somewhat later in making their appearance. "In embryos," he says, "$\frac{1}{14}$th of an inch in length (Pl. xxxvii. Fig. 6), I have found the cephalic portion of the blastoderm beginning to extend upwards again over the anterior face of the germ, so as to constitute its anterior and a small part of its superior wall. This portion is divided by a median fissure into two lobes, which play an important part in the development of the head, and will be termed the "procephalic lobes." I have already made use of this term for the corresponding parts in the embryos of *Crustacea*. The rudimentary thorax presents traces of a division into three segments; and the dorso-lateral margins of the cephalic blastoderm,

* "Lectures on the Anatomy, &c. of the Invertebrate Animals."

† "Untersuchungen uber die Entwickelung und den Bau der Gliederthiere," 1854.

‡ "Linnean Transactions," v. xxii. 1858.

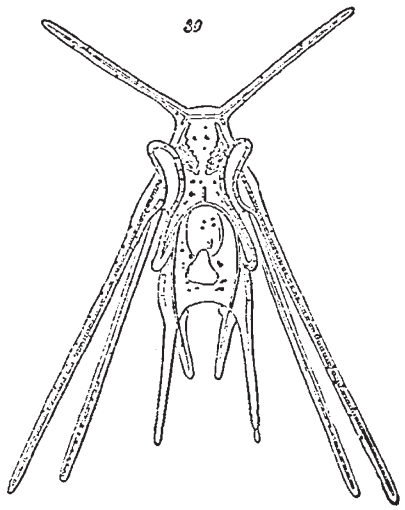

FIG. 39.—Larva of Echinocidaris, seen from above × $\frac{6}{5}$ (after J. Muller).

behind the procephalic lobes, have a sinuous margin. It is in embryos between this and $\frac{1}{100}$th of an inch in length, that the rudiments of the appendages make their appearance, and by the growth of the cephalic, thoracic, and abdominal blastoderm, curious changes are effected in the relative position of those regions."

In *Chrysopa oculata*, one of the Hemerobiidæ, Packard has described* and figured a stage in which the body segments have made their appearance, but in which "there are no indications of limbs. The primitive band," he says, "is fully formed, the protozorites being distinctly marked, the transverse impressed lines indicating the primitive segments being distinct, and the median furrow easily discerned." Here also, again, the dorsal walls are incomplete, and the internal organs as yet unformed.

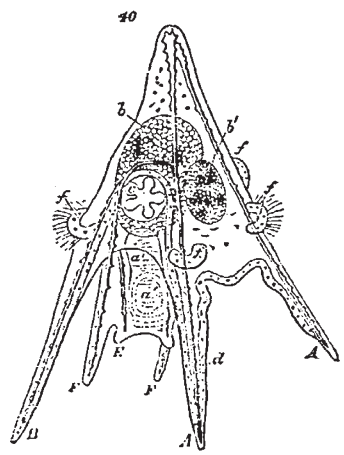

FIG. 40.—Larva of Echinus, × 100. *A*, anus; *F*, mouth process; *B*, posterior side arm; F_1, accessory arm of the mouth process; *a*, mouth; a^1, œsophagus; *b*, stomach; b^1, intestine; *o*, posterior orifice; *d*, ciliated bands; *f*, ciliated epaulets; *c*, disc of future Echinus (after J. Muller).

* "Embryological Studies on Hexapodous Insects." Peabody Academy Science. Third memoir.

In certain Dragonflies (Calypteryx), and Hemiptera (Hydrometra), the legs, according to Brandt,* appear at a still earlier stage.

According to the observations of Kolliker† it would appear that in Donacia the segments and appendages appear simultaneously. Kolliker himself, however, admits that "meæ de hoc insecto observationes satis sunt manca," and it is possible that he may never have met with an embryo in the state immediately preceding the appearance of the legs.

On the whole, as far as we can judge from the observations as yet recorded, it seems that in Homomorphous insects the ventral wall is developed and divided into segments before the appearance of the legs, but that the latter are formed simultaneously, or almost simultaneously, with the cephalic appendages, and before either the dorsal walls or the internal organs.

As it may be interesting from this point of view to compare the development of other Articulata with that of insects, I give a figure (Fig. 32) representing one of the early stages in the development of a spider (Pholcus) after Claparede,‡ who says, "C'est à ce moment qu' a lieu la formation des *protozorites* ou segments primordiaux du corps de l'embryon. Le rudiment ventral s'épaissit suivant six zônes disposées transversalement entre le capuchon anal et le capuchon céphalique. L'œuf considéré par sa face ventrale offre alors un contour à peu près circulaire et on peut le croire sphérique. Les zônes se montrent alors comme six circles d'un blanc plus éclatant, tracés sur la sphère."

Among Centipedes the development of Julus has been described by Newport.§ The first period, from the deposition of the egg to the gradual bursting of the shell, and exposure of the embryo within it, which, however, remains for some time longer in connection with the shell by a distinct funis, lasts for twenty-five days. The segments of the body, originally six in number, make their appearance on the twentieth day after the deposition of the egg, at which time there were no traces of legs. The larva when it leaves the egg is a soft, white, legless grub (Fig 33), consisting of a head and seven segments, the head being somewhat firmer in texture than the rest of the body. It exhibits rudimentary antennæ, but the legs are still only represented by very slight papilliform processes on the undersides of the segments to which they belong.

As already mentioned, I believe that at one time the vermiform state of the Homomorphous insects, which, as we have seen, is now so short, and passed through at so early a stage of development, was more important, more prolonged, and accompanied by a more complete condition of the internal organs. The compression, and even disappearance, of embryonal stages which are no longer adapted to the mode of life, which do not benefit the animal, is a phenomenon not without a parallel in other parts of the animal and even of the vegetable kingdom. Just as in language long compound words have a tendency to concision, and single letters sometimes linger on, indicating the history of a word, like the "l" in "alms," or the "b" in "debt," long after they have ceased to influence the sound; so in embryology useless stages, interesting as illustrations of past history, but without direct advantage under present conditions, are rapidly passed through, and even, as it would appear, in some cases altogether omitted.

For instance, among the Hydroida, in the great majority of cases, the egg produces a body more or less resembling the common Hydra of our ponds, and known technically as the "trophosome," which develops into the well-known Medusæ or jelly-fishes. The group, however, for which Prof. Allman has proposed the term Monopsea,* and of which the genus Egina may be taken as the type, is, as he says, "distinguished by the absence of a hydriform trophosome, the ovum becoming developed through direct metamorphosis into a medusiform body, just as in the other orders it is developed into a hydriform body." Figure 34 represents, after Allman, a colony of *Bougainvillea fruticosa* of the natural size. It is a British species, which is found growing on buoys, floating timber, &c., and, says Allman,† when in health and vigour, "offers a spectacle unsurpassed in interest by any other species—every branchlet crowned by its graceful hydranth, and budding with Medusæ in all stages of development (Fig. 35), some still in the condition of minute buds, in which no trace of the definite Medusa-form can yet be detected; others, in which the outlines of the Medusa can be distinctly traced within the transparent ectotheque; others, again, just casting off this thin outer pellicle, and others completely freed from it, struggling with convulsive efforts to break loose from the colony, and finally launched forth in the full enjoyment of their freedom into the surrounding water. I know of no form in which so many of the characteristic features of a typical hydroid are more finely expressed than in this beautiful species."

Figure 36 represents the Medusa form of this species, and the development thus described may be regarded as typical of the Hydroida; yet, as already mentioned, the Æginidæ do not present us with any stage corresponding to the fixed condition of Bougainvillea, but on the contrary are developed direct from the egg.

But on the other hand there are groups in which the Medusiform stage becomes less and less important.

Among the higher Crustacea again the great majority go through well-marked metamorphoses. Figs. 37 and 38 represent two stages in the development of the prawn. In the first (Fig. 37), representing the young animal as it quits the egg, the body is more or less oval and unsegmented, there is a median frontal eye, and three pairs of natatory feet, the first pair simple, the two posterior biramose. Very similar larvæ occur in various other groups of Crustacea.

They were at first regarded as mature forms, and O. F. Müller gave them the name of Nauplius. So, also, the second or Zoea form (Fig. 38) was at first regarded as a mature animal, until its true nature was discovered by Vaughan Thompson.

The Zoea form of larva differs from the perfect prawn or crab in the absence of the middle portion of the body and its appendages. The mandibles have no palpi, the maxillipeds or foot-jaws are used as feet, whereas in the mature form they serve as jaws. Branchiæ are either wanting or rudimentary, respiration being principally effected through the walls of the carapace. The abdomen and tail are destitute of appendages. The development of Zoea into the perfect animal has been well described by Mr. Spence Bate‡ in the case of the common crab (*Carcinus mœnas*).

All crabs, so far as we know, with the exception of a species of land crab (*Gegarcinus*), described by Westwood, pass through a stage more or less resembling that shown in Fig. 38. On the other hand the great group of Edriopthalma, comprising Amphipoda (shorehoppers, &c.) and Isopoda (woodlice, &c.), pass through no such metamorphoses; the development is direct, as in the Orthoptera. It is true that one species, *Tanais Dulongii*, though a typical Isopod in form and general character, is said to retain in some points, and especially in the mode of respiration, some peculiarities of the Zoea type; but this is quite an exceptional case. In Mysis, says F. Muller,§ "there is still a trace of the Nauplius-stage; being transferred back to a period when it had not to

* Mem de l'Acad. Impé. des Sci. de St. Petersburg." 1869.
† Observationes de Prima Insectorum Genesi, p. 14.
‡ Recherches sur l' Evolution des Araignées.
§ Philosophical Transactions, 1841.

* Monog. of the Gymnoblastic or Tubularian Hydroids. By G. J. Allman, F.R.S., &c., Roy. Society. † l.c., p. 315.
‡ Philosophical Transactions, 1859, p. 589.
§ "Facts for Darwin," Eng. Trans., p. 127.

provide for itself, the Nauplius has become degraded into a mere skin; in *Ligia* this larva-skin has lost the traces of limbs, and in *Philoscia* it is scarcely demonstrable."

Once more, the Echinodermata in most cases "go through a very well-marked metamorphosis, which often has more than one larval stage. The distinctive character of the metamorphosis appears to be the possession by the larvæ of at least a mouth and pharynx, which, whether absorbed or cast off, is never converted into the corresponding organs of the perfect Echinoderm developed inside of the provisional organism. The mass of more or less differentiated sarcode, of which the larva, or pseudembryo, as opposed to the Echinoderm within it, is made up, always carries upon its exterior certain bilaterally-arranged ciliated bands, by the action of which the whole organism is moved from place to place, and it may be strengthened by the superaddition to it of a framework of calcareous rods."*

Thus Fig. 39 represents a larva of *Echino-cidaris*, after Muller;† The body is transparent, $\frac{6}{100}$ in length, shaped somewhat like a double easel, but with two long horns in front, which, as well as the posterior processes, are supported by calcareous rods. These larvæ swim by means of minute vibratile hairs, or ciliæ. They have a mouth, stomach, and in fact, a well-defined alimentary canal, but no nerves or other organs have yet been discovered in them. After swimming about in this condition for awhile, they begin to show signs of change. An involution of the integument takes place on one side of the back, so as to form a pit or tube, which continues to deepen till it reaches a mass or store of what is called blastema, or, as we may say, the raw material of the animal body. This blastema then begins to grow, and gradually assumes the form of the perfect Echinoderm. In doing so it surrounds and adopts the stomach of the larva, but forms for itself a new mouth or gullet, throwing off the old mouth, together with the intestine, the calcareous rods, and in fact all the rest of the body of the larva.

Fig. 40 represents a larva probably of *Echinus lividus*, from the Mediterranean, and shows the commencement of the sea egg within the body of the larva. The capital letters denote the different arms, *a* is the mouth, *a'* the æsophagus, *b* the stomach, *b'* the intestine, *f* the ciliated lobes or epaulets, *c* the young sea-egg.

JOHN LUBBOCK

(*To be continued.*)

EXTIRPATION BY COLLECTORS OF RARE PLANTS AND ANIMALS

THE Legislature, having very properly provided for the preservation of small birds, might extend its protection to other animals and to plants; for although it would be inexpedient to prevent individuals from taking rare insects and botanical specimens, it is surely expedient to deter persons or societies from offering premiums which are leading to the extirpation of such species.

Some years ago a judicious and formal protest against this culpable practice was published by many of the most eminent British botanists, and it has constantly been deplored by all true lovers of natural science. The respected president (the Rev. Dr. Mitchinson) of our East Kent Natural History Society, in his address at the last annual meeting thereof at Canterbury, made such strong observations on the subject as might raise the question whether local societies may not do as much harm by promoting the extirpation of rare plants and animals as good in other respects; and I have always been insisting, at the meetings of the same society and elsewhere, that it is our duty to cherish, and not destroy the precious plants and animals of the district. Whenever a rare plant or animal is exhibited at those meetings, we have always a wail about its having been "not long since often seen, though now fast disappearing." A chief cause of this is the deplorable rapacity of collectors of and traffickers in specimens; since the preposterous notion prevails that botany and entomology consist in a recognition of the mere physiognomy, without the least regard to the physiology, of species, and being able to call them by their scientific names.

And so it will be while local societies continue to encourage such errors, instead of promulgating the essential principles of botanical or entomological science, and obstructing the injurious operations of mere collectors or pretenders. And this desirable end, so far as regards taxonomy, might be easily attained without the least harm to rare species. Prizes for the best display, illustrated by microscopic drawings and preparations of the generic and specific characters of sections or the whole of many natural orders would afford really good tests of the industry and attainments of the candidates. For example, why not try for this purpose the Willows, Grasses, or Sedges? Two of these orders have the further recommendation of being of great economic value. Again, as specific distinctions seem to be the ultimate aim of these societies, certain cells or tissues, such as the pollen, epidermis, hairs, and stomata, would afford good subjects for investigation in this point of view, as would also raphides and other plant-crystals, and very likely disclose valuable characters not yet recognised in the books of systematic botany.

I have been led to these remarks by the increasing frequency of the practice now deplored. As the "West Kent Natural History, Microscopical, and Photographic Society" is much and deservedly respected, and exercises justly considerable influence in its department, an extract from its last "Council's Report," p. 19, will suffice as a sample of the mischief:—"With a view to promote the study of Entomology and Botany among the members of the Society and their families, the Council, in the early part of the year, announced their intention of giving two prizes of 5*l.* 5*s.* each, one for the best Botanical collection, the other for the best collection of Lepidopterous Insects; all specimens to be gathered or taken within the West Kent district." This quotation is by no means intended for blame to any particular society, but merely as an example taken from one of the printed "Reports" that has lately reached me of what is still being sown broadcast generally throughout the country.

And here we have plainly not only a reward of money for the best collection of plants and Lepidoptera in a given district, but a temptation or inducement to unscrupulous collectors, in their anxiety to win the prize and defeat their competitors, to destroy such rare specimens as they may not take away. Such nefarious conduct is not meant to be insinuated of the West Kent Society; but my object is simply to assert that which I know has too often been the effect of such prizes, and to invoke the aid of NATURE in suppressing the evil.

GEORGE GULLIVER

A FRENCH PHYSICAL SOCIETY

THE scientific movement increases in France; it began about the end of the Empire, under the ministry of Durüy, and has since taken greater proportions, especially after the last war. The new French Association for the Advancement of Science,* it is well known, is modelled after the British Association, the success of which has surpassed expectation.

The physicists of Paris have assembled for several years in the laboratories of the Superior Normal School, placed at their disposal by M. Berlin, the director of the scientific studies of this school. They conversed about physics

* "Rolleston—"Forms of Animal Life," p. 146.

† Uber die Gattungen der Seeigellarven. Siebente Abhandlung. Kon. Akad. d. Wiss. zu Berlin. Von Joh. Müller, 1855, Pl. iii. fig. 3.

* See NATURE, vol. v. p. 357.