

The Larva of the Eel.

By

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Le Leptocefalide e la loro trasformazione in Murenide. Nota preliminare del Corr. G. B. Grassi e del dott S. Calandruccio. Atti d. R. Accad. d. Lincei, Ser. v, vol. i. Soluzione di un enigma antichissimo ossia. Scoperta della metamorfosi dell' anguilla. Grassi e Calandruccio. Neptunia, 15—30 Sett., 1894.

FROM the time of Aristotle many naturalists have desired, and a large number have attempted, to discover something about the breeding and development of the common eel, but until the present time it has remained a baffling mystery. At last the mystery is to a great extent penetrated; the larva of the eel has been discovered, and turns out to be a creature which was known before. Until the present year absolutely nothing was known of the history of the eel between the disappearance of the parents in the sea in autumn, and the appearance of the young transparent elvers in early spring. Professor Grassi and Dr. Calandruccio have now discovered that one of the larval forms called Leptocephali is the larva of the common eel. This form was described and distinguished as *Leptocephalus brevivirostris*, but it was not suspected that it belonged to the eel.

In my paper on the *Reproduction and Development of the Conger*, in No. 1, vol. ii, of this Journal, 1891, I gave some account of what was known at that time concerning the habits and history of the Leptocephali. I mentioned there that only one kind of Leptocephalus was known on the British coasts, namely, *L. Morrisii*, and that the transformation of a specimen of that kind into the conger had been observed at Roscoff, by M. Yves Delage. Leptocephali are most frequently captured at Messina, and it was largely from specimens obtained there that a number of different kinds were defined and described. In 1856 the Catalogue of Apodal Fish, drawn up by Professor Kaup, of Darmstadt, was published by the trustees of the British Museum. Its object was to give a description of all the genera and species of apodal fish, *i. e.* fish destitute of pelvic fins, existing in the various English and Continental collections. In this work the family Leptocephalidæ was defined as comprising small, compressed,

transparent fish, entirely devoid of scales, and having a very imperfect cartilaginous skeleton. The forms were distinguished into four genera,—*Esunculus*, *Hyoprurus*, *Tilurus*, and *Leptocephalus*. It must be remembered that in this work of Kaup's, as in much work of a similar kind, the method is purely empirical; specimens are described simply as they appear, and different forms are called different species without any consideration of the relations they may bear to each other, without regard to such questions as: are the specimens adult or larval? or: may not many of the different forms be the same animal at different ages or in different sexes? But even from the empirical descriptive point of view the inclusion of *Esunculus* in the *Leptocephalidæ*, or even among the apodal fishes at all, was a mistake, for it has distinct pelvic fins, and Kaup gives the number of fin-rays in these as five. It has short dorsal and ventral fins, nearly opposite to each other, and a forked caudal fin. It is obviously the larva of some fish belonging to a family other than the *Murænidæ*. It resembles somewhat a young *Clupeoid*, but not very closely; the head is smaller, the dorsal fin farther behind the pelvic. There were a large number of specimens of this form in the Paris Museum, but the place of their capture is not recorded.

Hyoprurus is a genus of which only one species was known, *H. Messinensis*, discovered by Gegenbaur at Messina, originally described by Kölliker. Kaup describes a single specimen, obtained like the others from Messina. The specimen was 4.96 inches long, and had a murænid continuous median fin extending round the body posteriorly, the extremity of the tail being pointed. The peculiarity of the genus is the sudden broadening of the body in the vertical plane immediately behind the head. The jaws are elongated and straight, with mere traces of teeth. Mr. Gill in his paper on the relations of the *Leptocephalids* in 1864 expressed the conclusion that *Hyoprurus* was the young stage of *Nettastoma melanurum*, a Mediterranean species of marine eel with a long and depressed snout, no pectoral fins, open gill apertures, and a tail twice as long as the body, tapering to a point. Dr. Günther in 1870 expressed his entire concurrence with this view.

Tilurus, of which two species were described by Kaup, is a much-elongated transparent compressed fish, also found at Messina. One specimen was 12.21 inches in length. The anus is situated near the end of the attenuated tail, which is as thin as a hair and coiled at its extremity. Dr. Günther was unable to refer *Tilurus* to any known fish, and thinks it does not belong to the *Murænidæ*.

Of *Leptocephalus* Kaup distinguished the following species:

Morrisii.—A blunt head, scarcely visible teeth; lateral line, belly,

and anal fin dotted with black points; tail pointed; greatest height one ninth of the total length.

Spalanzani.—Blunt head, almost imperceptible teeth; body narrower in proportion to length.

punctatus.—A round vermiform body; points along the lateral line, oblique pairs of dots along the edge of the belly; anus before the middle of the body, and a row of indistinct points on the anal fin. Specimen came from Messina.

diaphanus.—Anus nearly in the middle of the total length, dorsal fin commencing somewhat before the anus; 4·37 inches long. Also from Messina.

Köllikeri.—A blunt caudal fin with distinct rather long rays; body not higher vertically than the head. Also from Messina.

Gegenbauri.—Has a similar tail, but the height of the body is greater. Also from Messina.

Bibroni.—Similar to the last, but anus behind the middle of the body. From Messina.

Yarrellii.—Similar, but anus still further back. From Messina.

stenops.—Stout teeth and large eyes closely approximated to one another. Probably from Messina.

longirostris.—Has long jaws and distinct teeth, and the body broadening suddenly in the vertical plane behind the head. From Messina.

tænia.—A round head, large projecting globular eyes, short snout, much-elongated broad body. Specimens from India and the Maldives.

brevirostris.—No dots; fourteen teeth in each jaw; small slender tail sustained by visible rays; eyes black; total length 3·15 inches. Locality Messina.

He also distinguished *acuticaudatus*, *Dussumieri*, *dentex*, *marginatus*, *lineo-punctatus*, and *capensis*. In a later paper, published in 1860, Kaup identified *L. Spalanzani*, Risso, with *Morrisii*, and described two other species of *Leptocephalus* under the names *Haeckeli* and *Kefersteini*.

Kefersteini.—Seven roundish spots composed of points along the intestine; anus a little behind the middle of the body; head extremely small, with very fine teeth. From Messina.

Haeckeli.—Head small and pointed, tail only one eighth the length of the body. Resembles *brevirostris*, but the snout is longer, the body not so high, and the tail less pointed. From Messina.

In my former paper I referred to the remarks concerning *Leptocephalidæ* contained in Dr. Günther's Catalogue, vol. viii, p. 138. It is there suggested that *Myrus*, *Ophichthys*, and perhaps also *Muræna* have their *Leptocephaline* forms. Pointing out that

the question whether the Leptocephali were normal or abnormal larvæ could only be decided by investigation of living specimens, Dr. Günther abandons the practice of distinguishing different species among them, and merely groups together the known forms which appear to have a common origin, or which by their general similarity appear to be closely connected together. Thus he groups together *L. Morrisii*, *diaphanus*, *Bibroni*, *Gegenbauri*, *Köllikeri*, and *punctatus*. We shall see that in recognising *punctatus* as the more developed stage of *Morrisii*, Günther is proved by the researches of Grassi and Calandruccio to have been right, while many of the other forms grouped with *Morrisii* by Günther turn out to be the larvæ of adult forms closely allied to the conger.

It is a curious fact that Leptocephali which are rarely observed or captured in other places are not uncommon at Messina. Commenting on this fact in 1883, Bellotti, an Italian naturalist, maintained that it gave support to the view that these creatures were not normal larvæ, but abnormal overgrown individuals whose proper development had been arrested by exceptional conditions. This investigator had only been able to capture a few rare specimens at Genoa, Nice, and Naples, and none at all at Palermo, Catania, or Siracusa, which are near Messina. He surmised that the impetuous currents and the numerous whirlpools of the narrow Straits of Messina were the exceptional conditions which caused the larvæ of congeners, &c., to pass through an abnormal course of development. Until the normal development was known, arguments of this kind, as I have remarked in my previous paper, were of little importance.

Signore Grassi is an Italian naturalist who lives at Catania. He is one of those who devote themselves chiefly to the application of rigid scientific method to investigation in the department which used to be called natural history, and which it has been proposed to distinguish by the term bionomics. He has made himself famous recently by his marvellous discoveries concerning the life histories of the termites or white ants. In 1892 he published a brief account of some researches which he and Dr. Calandruccio had made on the Leptocephali. For five years they had noticed that these forms were common enough at Catania, being captured at all times of the year and sometimes in abundance. They were most plentiful in the harbour, and were caught by the nets called tartarene and sciabica, nets which are dragged over a sandy or muddy bottom. In these authors' opinion this abundance of Leptocephali at Catania is peculiar to the period mentioned, and to be attributed to the volcanic eruptions which have sent much lava into the sea, and so compelled certain Murænidæ to leave their usual haunts among the

rocks or at great depths and seek shallower water. It is obvious that this suggestion has no great air of probability.

The careful experimental investigation of the Leptocephali was carried on by these naturalists in the year 1891-2, and the following were the results. In the development of the conger (*Conger vulgaris*) three stages can be distinguished:—First, a tænioid form resembling *L. Morrisii*, except that the dots on the lateral line are limited to the posterior extremity of the body; second, *L. Morrisii* itself; and third, the form which had been previously distinguished as *L. punctatus*: from this the perfect conger is directly developed. The first tænioid form has long and fine larval teeth; these are wanting in *Morrisii*, in which the permanent teeth begin to develop in a position internal to that of the larval.

During the metamorphosis there takes place a gradual reabsorption of the gelatinous skeleton, much pigment develops, the anus passes into a more anterior position, and so much diminution in size takes place that from larvæ 12½ cm. long (5 inches) are obtained congers only 7½ cm. (3 inches). During the transformation, which may not take more than a month, the Leptocephali take no food or only minute particles. The transformation may be followed without any difficulty in specimens kept in any aquarium, or even in tubs; the authors observed it in 150 individuals. This is surely a sufficient confirmation of the isolated observation of Delage. All the various stages observed in captive specimens were also seen in specimens taken from the sea. In the aquaria the larvæ hid away in groups, threaded through the crevices under stones, the eggs of *Aplysia*, &c.; they also sought the darkest corners of the aquaria and avoided the light.

L. diaphanus of Kaup was found to develop into *Congromuræna balearica*. This is a Mediterranean species of *Congromuræna*, a genus very similar to *Conger*, but distinguished by the presence of large muciferous cavities in the front part of the skull, and the dorsal fin commencing at a more anterior point, namely, nearly above the gill opening. *L. Köllikeri* proved to be the larva of *Congromuræna mystax*, the only other Mediterranean species of the genus; and *L. Haeckeli*, *Yarrellii*, *Bibroni*, *Gegenbauri*, and probably *brevirostris* were found to be merely different stages in the development of the same form. The investigators have now come to a different conclusion concerning *brevirostris*, but with regard to the others reference to Kaup's original descriptions and figures shows that they resemble one another in the truncated, rather broad form of the tail and its distinct rays. In the course of development it appears that the post-anal or caudal portion of the body continually grows longer in proportion to the pre-anal or anterior portion. It

thus appears that the Leptocephaline forms grouped with *Morrisii* by Günther are larval stages of Conger and Congromuræna, and his view of their close connection is shown to have been remarkably sound.

L. Kefersteini was found to be a somewhat rare form at Catania, but it was easily kept alive in aquaria, where it buried itself in the sand at the bottom and changed into *Ophichthys serpens*. *Ophichthys* is distinguished chiefly by having the extremity of the tail free, not surrounded by the median fin, and a pointed snout projecting beyond the lower jaw. *L. stenops* was found to be the larva of *Myrus vulgaris*, whose characters are—nostrils on or close to the margin of the upper lip, caudal rays very short, tail twice as long as the trunk, white lines across the occiput, and white pores on the face and lateral line. *L. longirostris* was similarly connected with Muræna, which has narrow gill openings, and a body suddenly becoming very thick just behind the head. This character is markedly exhibited by the larva. *L. tænia* is probably the larva of Sphagebranchus, which is allied to *Ophichthys* (united with it by Günther), but has the gill openings convergent on the ventral surface of the head.

The same naturalists, pursuing their researches on the Leptocephali, have now satisfied themselves that the species *L. brevirostris* is the larva of the common eel. They have not, it is true, been able to follow the entire transformation on one and the same specimen, but they have verified the most important changes in several individuals, and have compared all the organs in these stages and in the perfect form, and have traced a gradual transition from the structure and characters of *brevirostris* to the fresh-water eel. *L. brevirostris* (Fig. 1) is a comparatively small Leptocephalid,

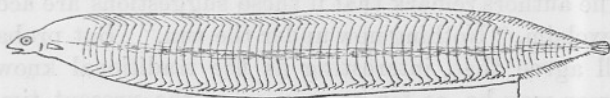


FIG. 1.—*Leptocephalus brevirostris*, after fig. 15, pl. xviii, of Kaup's Catalogue of Apodal Fish in the British Museum, 1856.

scarcely reaching the maximum length of 8 cm. ($3\frac{1}{4}$ inches), with a maximum vertical height of 1 cm. The reduction in length during the metamorphosis may be somewhat more or somewhat less in different individuals, but never exceeds 3 cm.; that is to say, a fully transformed young eel, which is still very transparent, may be as short as 5 cm. (2 inches), but not less, and it is very slender.

L. brevirostris has not hitherto been found anywhere else except in the Straits of Messina. Is it possible, ask the Sicilian naturalists, that eels undergo a metamorphosis only in that place, and elsewhere have a different history? The hypothesis is exceedingly improbable. They have made investigations, and convinced themselves that nowhere

can young eels be obtained which are less than 5 cm. long. Contrary assertions are to be found in literature. It has been asserted that there are eels only 2 or 3 cm. long, or even as small as 7 mm. (about $\frac{3}{8}$ inch), but critical examination shows that no such statements rest on direct observation. The *Leptocephali brevirostres*, which are the larvæ of the eel, have hitherto escaped observation in other places on account of their habit of hiding themselves in the bottom of the sea.

The authors add some curious remarks concerning the history of the knowledge of the subject. They tell us that it is a fact that the fishermen of Augusta know by tradition the metamorphosis of the Murænidæ, by which we presume is meant that they have a tradition that *Leptocephali* are the immature or larval forms of congers and eels. It is also a fact that at Catania the *Leptocephali* are commonly called *Morenelle*, or little Murænæ. It is to be inferred that from time to time some observant fishermen have noticed similarities or transition stages which led them to express this conclusion among their fellows.

Aristotle states, in his History of Animals, that eels have no sexes, nor eggs, nor semen, and that they arise from γῆς ἐντέρα, the entrails of the earth. By this expression some have understood earthworms, others have maintained that the Greeks applied it to all sorts of creeping, limbless creatures living in soil or mud, and believed that these were spontaneously generated. At Palermo the *Leptocephali* are called *lombrici* or *vermicelli di mare*, and Grassi and his colleague suggest that perhaps the belief that these *lombrici* gave rise to Murænids reached Aristotle in some form or other, and so caused him to write that eels arose from the entrails of the earth. The authors remark that if these suggestions are accepted we may well exclaim, "Nothing new under the sun." But probably most people will agree that, interesting as the traditional knowledge of the fishermen may be, as far as science in the present time is concerned, the knowledge of the transformation of the eel and other Murænidæ is due to the patient and fruitful investigations of Grassi and Calandruccio.

Considering that eels are so common, it will be a matter of much interest to make renewed attempts to discover their larvæ and those of the conger at Plymouth, and at other places outside the Mediterranean. The subject suggests two interesting questions: firstly, are *Leptocephali* pelagic or not, or are some pelagic and some not? secondly, are the eggs of the Murænidæ pelagic, or some pelagic and some not, as in other families of fishes? It appears from the account given by Grassi and Calandruccio that the *Leptocephali* at Catania are captured on the bottom, and we have just seen that these authors conclude that the larva of the eel has escaped capture

in other places from its habit of hiding or burrowing in the sea bottom. In captivity the larva of the conger was found to hide at the bottom and avoid the light. *L. Kefersteini*, the larva of *Ophichthys serpens*, lived in the aquarium buried in the sand; and the larva of *Congromuræna balearica* also burrowed into the sand, although, singularly enough, it could only be kept alive on a naked marble bottom. We are not told whether these larvæ came out at night and swam about freely. That the larvæ of the conger and common eel are not constantly pelagic at night seems proved by the fact that they have never been taken in abundance in nocturnal tow-netting expeditions. I conclude, therefore, that these Leptocephali, and all those known from the Mediterranean, are not truly pelagic, but live on or in the sea bottom, and that the reason they are found in the open water or at the surface at Messina is that there the strong tidal currents and eddies stir up the bottom and carry their light bodies about as scraps of paper are lifted and borne along by the wind. Reference to my previous paper, and the records which are there cited, will show that in two cases *L. Morrisii* has been taken in a hand-net near the surface of the water, but in other cases it was taken from the bottom,—for instance, in the process of fishing for prawns. There can be little doubt that the larvæ of the conger and of the eel exist around our coasts in great abundance, under stones or buried in sand or gravel, and that we do not catch them because we do not know the right way to go about it.

But, on the other hand, we find constantly in narratives of oceanic zoological researches that Leptocephali were taken in abundance in ordinary tow-nets worked near the surface. This, it is to be remarked, occurs always in the tropics. For instance Giglioli and Issel, in their volume *Pelagos*, published in 1884, state that twice only during the voyage of the "Magenta" they found specimens of *Leptocephalus* in the pelagic net, once in sight of Java, once in the South Pacific.

In the "Challenger" narrative the occurrence of pelagic Leptocephali is only mentioned twice, once in the account of pelagic animals observed between Fernando Noronha and Bahia, off the coast of Brazil, 5° to 15° south latitude, the second time among those captured on the voyage from the New Hebrides to New York, in about the same latitude to the eastward of Australia in the Pacific. In the former case the Leptocephali were accompanied by the Pleuronectid larva of *Rhomboidichthys*, the larva originally known as *Plagusia*, characterised by the peculiarity that the lower eye reaches the upper surface by passing through the base of the dorsal fin. Dr. Günther gives the following account of the Leptocephali in his Report on the Pelagic Fishes of the "Challenger." He says that

singularly few specimens were collected during the expedition, and these throw no new light on the question of origin. Six specimens obtained in mid-Atlantic belong to the form which has received the name *pellucidus* and other names. These other names are those associated by Grassi with *Congromuræna mystax*. One specimen obtained on the west coast of Africa at the surface belonged to the form *L. Morrisii*. Another, from a station near the Admiralty Islands, belonged to the form *L. tænia*. Lastly, a specimen from the North Atlantic had the characters of *L. brevirostris*. It is much to be regretted that no further description or any figures are given. If the comparisons are correct, it would follow that the larva of both the common conger and common eel were taken in the open Atlantic in a pelagic condition.

A. Agassiz remarks in Three Cruises of the "Blake," vol. i, p. 121, that we may trace the northern course of the Gulf Stream by the presence of Sargassum, Porpita, Leptocephali, &c., which are carried each year to the coast of Southern New England.

It seems evident that in tropical regions of the ocean truly pelagic Leptocephali are of constant occurrence and fairly abundant. It will probably be found that these are the larvæ of species of Murænidæ other than those whose larvæ have been traced by the Sicilian naturalists. But in the present state of our knowledge it seems impossible to distinguish satisfactorily the oceanic pelagic forms from those of the Mediterranean, or from those which are not pelagic. Thus Grassi and Calandruccio suggest that *L. tænia* is the larva of species of Sphagebranchus, of which species occur both in the Mediterranean and the East Indies. But the names *tænia*, *marginatus*, *lineo-punctatus*, and *capensis* are grouped together by Günther as applying to much-elongated forms which appear to have been taken at the surface of the open ocean: some specimens reach a length of 25 cm., or nearly 10 inches. The specimens named *L. tænia* by Kaup came from India and the Maldivé Islands, but we are not told whether they were pelagic; probably they were. If so, the question arises whether the form called *L. tænia* by the Sicilians is also truly pelagic, or if it belongs to a different species. It would scarcely be profitable to pursue these speculations further. What has been said is sufficient to suggest strongly that the characters and history of the Leptocephali still offer a most promising field of study and investigation, alike in the Mediterranean, in the tropics, and on our own coasts. It is much to be hoped that Drs. Grassi and Calandruccio will publish a complete account of their observations with satisfactory figures, in order to satisfy the interest and curiosity excited by their preliminary communications. It is worthy of remark that there is some similarity between the cases of

the Leptocephali and the larval Pleuronectid originally described by Steenstrup as *Plagusia*, and probably belonging to the genus *Rhomboidichthys*. This larva is a conspicuous pelagic form in tropical seas on account of its large size, and in this respect and in its oceanic distribution differs from the smaller larvæ of other genera which are abundant on temperate shores, but whose pelagic life is but little prolonged. In like manner it will probably be found that the oceanic Leptocephali are peculiar to certain special genera among the *Muraenidæ*. In the article printed in *Neptunia*, the Sicilian ichthyologists make no mention of the well-known oceanic Leptocephali, and have overlooked their existence in formulating their general conclusion that these larvæ escape notice and capture by their habit of hiding at the bottom, except at Messina and Catania.

With regard to the pelagic condition of the ova of *Muraenidæ*, Grassi and Calandruccio state that they have been able from their own observations to confirm with complete certainty the suggestion of Raffaele that certain pelagic eggs described by him belong to this family. But they do not assert that they have identified particular eggs with particular species. If the eggs of the conger and common eel are really pelagic, it is an inexplicable fact that they have not been identified in the course of the careful and long-continued researches made on pelagic ova at Plymouth and other places on the Atlantic coasts of Europe.