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I KOMMISSION HOS C. A. REITZEL
BIANCO LUNOS BOGTRYKKERI
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CONTENTS

I. Introduction

In the "First Report on Eel Investigations", vol. XVIII des Rapports et Procès-Verbaux du Conseil International pour l'Exploration de la Mer", published on the 25th of November 1913, I have set forth the results which I considered as having been obtained by my work in connection with classification of the European, American and Japanese fresh-water eels, at the same time making mention of the fact that the characterization of the species necessitated the examination of a great number of specimens. As regards the characters to be considered in distinguishing the species, these were divided into two classes; a) permanent characters, comprising those which are present in their ultimate form at a very early stage in the life of the fish, and b) variable characters, being those which in the course of growth are subject to greater or lesser alteration. Owing to the very considerable labour involved by investigation of hundreds or thousands of specimens, I had not been able to thoroughly examine more than a few of the characters in question. These were, 1) The number of vertebrae, a permanent character, and 2) the ano-dorsal distance, or distance between the initial points of the dorsal and anal fins, expressed as a percentage of the total length, which is a variable character. Detailed investigation of these two characters showed that both were of systematic importance. Countings of vertebrae enabled us to prove, that the European, American and Japanese eels belong to three different species. Only in the case of the first-named was sufficient material available to permit of more thorough investigation, and discussion of the important question as to whether or no several "smaller species" or "races" could be shown to exist within this species. With regard to this, I arrived at the following result:

Countings of vertebrae of numerous specimens from different localities within the area of occurrence of the European eel seem to indicate that we have everywhere to deal with one and the same species. This is suggested, partly by the high degree of uniformity between the different samples, the averages of which exhibit but slight variation, and partly by the fact that the slight variation occurring is entirely independent of the geographical distribution of the samples within the great area extending from Iceland to the eastern waters of the Mediterranean.

A comparative investigation of the ano-dorsal distance for a large number of samples shows a slight increase in the value of $\frac{a-d}{t} \cdot 100$ from north to south. The immediate cause or causes of this peculiarity I was not able to ascertain; I did, however, arrive at the conclusion that it seems impossible to split up *Anguilla vulgaris* into two or more races on the basis of this variation, since the extreme values are gradually connected by all intermediate values. Of other variable characters, the length of the head $\left(\frac{h}{t} \cdot 100\right)$ and the length of the elver stage were briefly referred to.

In the first report, the investigations there described were expressly designated as a first contribution towards the solution of the problem in question, and it was predicted that several other characters would have to be included in the work before this could be expected to furnish any definite result.

The present work is thus a continuation and amplification of the investigations commenced in the first as to the classification of the fresh-water eel. The same three species are here dealt with: *Anguilla vulgaris*, *Anguilla rostrata* and *Anguilla japonica*. In the case of the American species, the material has been essentially increased, a large sample of elvers collected at W. Gloucester, Mass. in May 1913 by Mr. W. W. Welsh having been received from Dr. Hugh M. Smith of Washington D. C., U. S. A. Thanks to this sample, I have been able to deal with the American eel far more thoroughly than hitherto. Further assistance in this respect has also been furnished by a small sample of elvers and young eels collected at the beginning of 1914 by the staff of the Danish Commission for the Investigation of the Sea at St. Croix, in the Danish West Indies.

In the rest, the material employed has been essentially the same as that on which the frequently mentioned Report was based. This last, however, was chiefly concerned with two characters, viz.: the number of vertebrae, and $\frac{a-d}{t} \cdot 100$ [1]) whereas in the present treatise, a number of other characters have been included. By this means, the results have been rendered considerably more reliable.

The characters here particularly dealt with are the so-called permanent characters, (for definition of the term, *vide* Report I, p. 4—5). These are as follows:

1) Number of vertebrae (supplementary to the matter contained in Report I, 1913).
2) Number of anal rays.
3) Number of branchiostegal rays.
4) Number of pectoral rays.
5) Number of caudal rays.

I will now proceed to the results obtained by investigation of the different characters. It should here be mentioned, that all the measurements have been made by myself, the necessary calculations having been undertaken by cand. mag. Aa. Strubberg and Frk. cand. mag. Kirstine Smith.

II. The Characters investigated

1. Number of vertebrae

In Report I, 1913, the number of vertebrae has been exhaustively dealt with; only, however, in the case of the European eel, the material available as regards the other two species being then but scanty. The large sample of elvers from W. Gloucester, Mass. U. S. A., referred to in the introduction, has therefore also been employed for countings of vertebrae, with a view to obtaining a more comprehensive view of the variation in number of vertebrae for the American eel than has hitherto been possible. A sample consisting of 502 specimens was taken, and the number of vertebrae determined for each. The result will be seen in the accompanying Table I, which further includes a summary of all countings of vertebrae of eels from the American continent and the West Indies. It will be seen from the table, that the figure 111, which had not previously been found in the case of the American eel, occurs three times in the W. Gloucester sample, which, however, lacks the figure 103 found once in the earlier material consisting of 361 specimens. From all countings, of 863 specimens in all, we thus find (*vide* Table I, summary), that the number of vertebrae in the American eel varies from 103 to 111, the figure of most frequent occurrence being 107, the next in order being 108 and 106.

The number of vertebrae is an excellent character by which to distinguish between the two species of *Anguilla* which occur in the region of the Atlantic. An idea of this may be obtained from Table II, showing the number of vertebrae in the first 266 specimens of the large elver sample from W. Gloucester, Mass., U. S. A. as compared with an equally large sample of elvers from Denmark examined for the purpose. From this we see, that only one figure is common to both species, viz.; 111. This occurs but three times in the total of 532 specimens contained in both samples together. This is to say, that a mixed sample of *Anguilla vulgaris* and *A. ro-*

[1] Other characters were, however, occasionally referred to, as for instance the length of the leptocephalus stage (p. 25) and the elver stage (p. 23), the length of the head (p. 21) the number of pectoral rays (p. 6) and anal rays (p. 6).

Table I. No. of vertebrae in the American eel *(Anguilla rostrata)*.

No. of vertebrae	No. of specimens	
	1 W. Gloucester, Mass., U. S. A., May 1913	2 Summary of all countings
111	3	3
110	19	31
109	61	96
108	131	221
107	162	274
106	107	184
105	16	45
104	3	8
103	...	1
Total No. of specimens	502	863
Average No. of vertebrae	**107·347**	**107·250**
σ (Standard deviation)	± 1·209	± 1·242
P. E. A, (Probable error of average)	± 0·0346	± 0·0285
P. F. A. (Probable fluctuation of average)	107·165 — 107·529	107·107—107·393

Table II. No. of vertebrae in 266 European and 266 American eels.

No. of vertebrae	No. of specimens	
	1 Nykjøbing, Sealand, Denmark, 1911	2 W. Gloucester, Mass., U. S. A., 1913
119	1	...
118	5	...
117	19	...
116	46	...
115	82	...
114	71	...
113	31	...
112	9	...
111	2	1
110	...	7
109	...	29
108	...	66
107	...	90
106	...	59
105	...	12
104	...	2
Average	**114·680**	**107·226**
σ (Standard deviation)	± 1·280	± 1·185
P. E. A. (Probable error of average)	± 0·0529	± 0·0490
P. F. A. (Probable fluctuation of average)	114·415 — 114·945	106·981 — 107·471

strata, amounting to 532 individuals in all, would contain but 0·56 % of specimens which could not be distinguished with perfect certainty, which again practically means that even single specimens of either species may always be classified by the number of vertebrae. As will subsequently be seen, this is generally impossible with other characters, even though the averages for these, as determined by examination of numerous specimens, may differ greatly for the two species.

2. Number of anal rays

In Report I, 1913, p. 5, mention is made of the fact that the number of anal rays is very large and variable; that they may be very difficult to count with accuracy, and that these purely practical difficulties had induced me hitherto to dispense for the most part with the fin-rays, though I did not doubt that the number of rays might characterize the species.

These difficulties have now been partly overcome by the employment of well preserved specimens of elvers stained with alizarine. By this means, the rays, or at any rate their basal parts, in the unpaired fins are rendered so distinct as to permit of their number being determined with absolute certainty, though it will naturally always be a lengthy and laborious task to procure checked countings of elements occurring in such great numbers. In addition to this, the difficulties may be greatly increased if the staining, for some reason or another, should not be completely successful. The prepared specimens of European elvers were quite satisfactory from a technical point of view, whereas in the only two samples available of American and Japanese elvers, the staining of the anal rays was for the most part but poor, which rendered the work of counting far more difficult.

The material examined consisted of 1,365 European, 245 American and 73 Japanese elvers. The result of the countings is shown in Table III. From this it will be seen, that the series of figures obtained for the three species overlap. Closer examination shows that *Anguilla rostrata* has the lowest values, *Anguilla japonica* the highest, the majority of variants in the case of the first falling below, in that of the last above 215[1]), whereas *Anguilla vulgaris* occupies an intermediate position, with approximately equal numbers of variants above and below 215. Similarly, we find that the lowest average is that of *A. rostrata*, (198·649), the highest that for *A. japonica* (220·26), whereas the average figure for *A. vulgaris*, (215·224) is intermediary, lying nearest, however, to that of *A. japonica*.

The table shows, in addition to the average for each sample, also σ (standard deviation), P. E. A. (probable error of average), and P. F. A. (probable fluctuation of average). This last is, as in Report I, 1913, calculated by multiplying the probable error by 5, and thus indicates with a probability of 1300—1400 to 1 the limits within which the actual average of an unlimited number of specimens of the single groups would lie.

We see from the table, that *A. rostrata* differs decidedly both from *A. vulgaris* and *A. japonica*, its P. F. A. lying quite outside that of the two others. On the other hand, *A. vulgaris* and *A. japonica* resemble each other more. Nevertheless, the average in the case of *A. japonica* (220·26) is far outside the P. F. A. of *A. vulgaris* (214·223—216·225). The wide range of the P. F. A. of *A. japonica* (216·13—224·39), owing to which the P. F. A. of the two species are not entirely distinct is doubtless merely due to the paucity of the Japanese sample as compared with the European (73 as against 1,365). Even a comparatively slight increase in the number of specimens of *A. japonica* would, to judge by the experience gained in all other similar countings, limit the P. F. A. for this species, so as to let the P. F. A. of the two species fall clear of each other.

We have thus seen, that the average number of anal rays, like that of the vertebrae, reveals a distinct difference between the European, American and Japanese eels. We have now to consider whether local "races" or "smaller species" can, by the aid of this character, be proved to exist within

[1] It must be regarded as due to mere chance, that no variants below 200 have been found in the case of *A. japonica*; the material however, consisting of only 73 specimens, is very small in comparison with that for the other two species examined, especially *A. vulgaris*.

each of these species. This point has been investigated only in the case of the European eel, owing to the inadequate amount of material available for the other two species.

The samples selected for investigation were taken from the most widely differing localities whence it was possible to obtain such; viz; a Baltic (Sealand, Denmark), an Atlantic (Bristol Channel, England) and a Mediterranean (Cette, France). The detailed results are given in Table III, 1—3. The averages for the three samples are, for Denmark 215·176, England 215·257, and France 215·24. Considering the extremely wide range of variation, 72, 62, 71 for the three samples, the averages lie surprisingly near each other; so near, as to render it immediately obvious that no racial difference can be shown to exist among the European eels by means of the number of anal rays. Examination of the P. F. A. for the three samples, as well as the fact that the average for the Mediterranean sample lies midway between the values for the two from northern Europe, both prove this to be the case.

The anal rays are, like the vertebrae, present or distinctly forming in their full number at a very early stage in the life of the individual. This may be seen from the very extensive material of growing larval stages procured by "Kommissionen for Havundersøgelser" in the course of a cruise made in the Atlantic by the M/S "Margrethe" in 1913. This material shows, that the larvae of the European eel have already at a length of some 4 cm. their full number of anal rays[1]).

The number of dorsal rays has not been subjected to closer investigation; although there is hardly any doubt that they may be used for the characterization of species in the same way as the anal rays. That they have not here been thus employed is due to the fact that the still greater number of rays in the dorsal fin would render the work even more difficult than in the case of the anal, in addition to which, the foremost rays in this fin are small, and frequently difficult to count with certainty.

3. Number of branchiostegal rays

Owing to the small number of variants, the branchiostegal rays would at first sight appear but poorly suited to the purpose of characterizing species. On the other hand, they are peculiarly susceptible to the alizarine staining process, which fact, together with the smallness of the number, renders it possible to rapidly and easily deal with a large amount of material. For this reason, they have been included in the present work.

The investigations, which comprised the branchiostegal rays of both right and left sides, (for results, *vide* Table IV, A and B) showed that these rays, despite the smallness of their number (8—13), may exhibit considerable numerical variation. True, the figure 11 is in all samples that of most frequent occurrence; the distribution of the remaining variants, however, exhibits characteristic differences. Worthy of note is also the fact that a difference of one ray may frequently be found between the right and left sides of one and the same specimen. There is no definite rule as to which side in such cases has the greater number; this falls, however, in most cases to the right, as is evidenced by the somewhat higher average for this as compared with the left. In comparing samples from different localities therefore, the rays of the right and left sides should be separately dealt with, as has been done in the table, (IV, A—B).

The table shows the averages for *A. vulgaris* (1—3), *A. rostrata* (4) and *A. japonica* (5) as for the right side 10·777, 11·025 and 11·265 respectively, i. e., lowest for the European, highest for the Japanese. The material in the case of *A. japonica* is but small (83 specimens) whereas in the case of the other two species it is considerable

[1] The following data regarding the larvae of the European eel may here be given: One specimen of 30 mm length exhibited a very large part of the fin where forming rays could not yet be distinguished. In the case of three specimens of 36, 37 and 38 mm were counted 201, 183 and 209 rays respectively; in the foremost part of the fin, however, the rays (or interspinous rays) were not yet forming, or at least, not to be counted with certainty. In the following 5 specimens, all the rays were apparently forming; length: 40, 41, 43, 47, 50 mm, with 215, 226, 213, 205 and 223 rays respectively. It may be added, that the full number of segments is present at an even earlier stage. This it was possible to determine, both in the case of *A. vulgaris* and *A. rostrata*, in larvae of abt. 2 cm in length, not, however, in those 1—1½ cm long.

Table III. No. of anal rays in *Anguilla vulgaris*, *A. rostrata* and *A. japonica*

No. of rays	No. of specimens					
	Anguilla vulgaris				A. rostrata	A. japonica
	1 Nykjøbing, Sealand, Denmark	2 Bristol Channel, England	3 Cette, France	1—3 Total	4 W. Gloucester, Mass., U. S. A.	5 Kyushyu S. Japan
253	...	...	...	...	...	1
252	...	...	...	...	...	...
251	...	...	...	...	...	...
250	...	...	...	...	...	...
249	...	...	1	1	...	...
248	...	1	...	1	...	...
247	1	...	3	4	...	...
246	...	1	...	1	...	...
245	1	...	1	2	...	...
244	1	...	...	1	...	1
243	...	...	...	...	...	...
242	1	1	...	2	...	...
241	1	...	2	3	...	...
240	2	1	2	5	...	...
239	1	2	4	7	...	...
238	3	1	2	6	...	1
237	2	3	3	8	...	2
236	3	2	2	7	...	...
235	6	3	3	12	...	...
234	6	5	4	15	...	3
233	3	2	4	9	...	4
232	2	4	3	9	...	2
231	6	3	4	13	...	2
230	8	5	8	21	...	...
229	6	7	6	19	1	2
228	9	10	8	27	...	...
227	11	10	9	30	...	2
226	11	9	8	28	...	2
225	13	10	11	34	...	...
224	13	15	8	36	...	2
223	11	16	13	40	...	1
222	14	12	13	39	1	3
221	18	12	15	45	1	2
220	19	19	12	50	2	2
219	17	14	18	49	...	3
218	10	24	22	56	2	6
217	13	19	15	47	2	4
216	12	14	14	40	4	1
215	15	21	17	53	...	3
214	16	16	15	47	3	4
213	20	17	15	52	4	4
212	14	10	20	44	4	3
211	14	18	17	49	6	3
210	11	13	14	38	6	2
209	10	15	13	38	3	2

208	13	15	12	40	5	..
207	9	16	12	37	7	1
206	11	11	16	38	8	...
205	10	11	14	35	8	...
204	12	5	12	29	8	1
203	10	9	6	25	9	1
202	8	9	10	27	12	2
201	9	9	5	23	10	...
200	8	6	6	20	11	1
199	8	6	7	21	8	...
198	6	4	7	17	11	...
197	5	5	5	15	10	...
196	3	4	...	7	7	...
195	2	2	5	9	10	...
194	3	2	...	5	9	...
193	3	2	2	7	4	...
192	2	2	1	5	6	...
191	2	...	...	2	10	...
190	2	...	1	3	10	...
189	...	1	1	2	3	...
188	2	...	2	4	6	...
187	...	1	...	1	5	...
186	1	...	...	1	4	...
185	...	...	...	...	6	...
184	...	...	1	1	5	...
183	...	...	...	...	4	...
182	1	...	...	1	2	...
181	...	...	...	...	2	...
180	...	...	...	...	...	...
179	...	...	1	1	1	...
178	...	...	...	...	1	...
177	...	...	...	...	2	...
176	1	...	...	1	1	...
175	...	...	...	...	...	...
174	...	...	...	...	...	...
173	...	...	...	...	...	...
172	...	...	...	...	...	...
171	...	...	...	...	...	...
170	...	...	...	...	...	...
169	...	...	...	...	...	...
168	...	...	...	...	...	...
167	...	...	...	...	1	...
166	...	...	...	...	...	...
Total No. of specimens	455	455	455	1365	245	73
Average No. of rays	**215·176**	**215·257**	**215·24**	**215·224**	**198·649**	**220·26**
σ (Standard deviation)	± 11·557	± 10·227	± 11·120	± 10·973	± 9·933	±10·46
P. E. A. (Probable error of average)	± 0·365	± 0·323	± 0·352	± 0.2003	± 0·428	± 0·826
P. F. A. (Probable fluctuation of average)	213·349—217·003	213·640—216·874	213·482—216·998	214·223—216·225	196·509—200·789	216·13—224·39

Table IV. No. of branchiostegal rays in *Anguilla vulgaris, A. rostrata* and *A. japonica*

A. Rays from right side

No. of rays	No. of specimens					
	Anguilla vulgaris				A. rostrata	A. japonica
	1 Nykjøbing, Sealand, Denmark	2 Bristol Channel, England	3 Cette, France	1—3 Total	4 W. Gloucester, Mass., U. S. A.	5 Kyushyu, S. Japan
13	...	1	4	5	12	1
12	101	52	53	206	170	27
11	300	226	253	779	406	48
10	194	147	164	505	153	7
9	12	9	4	25	11	...
Total No. of specimens	607	435	478	1520	752	83
Average No. of rays	**10·807**	**10·745**	**10·768**	**10·777**	**11·025**	**11·265**
σ (Standard deviation)	±0·727	±0·697	±0·684	±0·705	±0·743	±0·626
P. E. A. (Probable error of average)	±0·0199	±0·0225	±0·0211	±0 0122	±0·0183	±0·0464
P. F. A. (Probable fluctuation of average)	10·707—10·907	10·637—10·857	10·663—10·873	10·716—10 838	10·934—11·116	11·03—11·50

B. Rays from left side

No. of rays	1	2	3	1—3	4	5
13	3	2	3	8	9	...
12	87	44	49	180	159	23
11	317	220	257	794	416	50
10	179	152	167	498	152	7
9	12	10	6	28	10	...
8	1	...	...	1	...	...
Total No. of specimens	599	428	482	1509	746	80
Average No. of rays	**10·811**	**10·7103**	**10·743**	**10·761**	**11·007**	**11·20**
σ (Standard deviation)	±0·724	±0·698	±0·677	±·703	±0·721	±0·582
P. E. A. (Probable error of average)	±0·0200	±0·0228	±0·0208	±0·0122	±0·0178	±0·044
P. F. A. (Probable fluctuation of average)	10·712—10·911	10·596—10·824	10·639—10·847	10·700—10·821	10·918—11·096	10·98—11·42

(1520 and 752). Despite the fact that the difference between the averages is but slight, we yet find that there is a difference, as regards the number of branchiostegal rays, between the European, American, and Japanese eels. The probable fluctuation of the average (P. F. A.) is here determined with peculiar accuracy. We find, that the true average for *A. vulgaris* lies between 10·716 and 10·838, for *A. rostrata* between 10·934 and 11·116, so that the two fluctuations do not overlap. It may be as well here to point out that this is equivalent to a probability of 1400 to 1 in favour of the two species differing as regards the number of branchiostegal rays.

As already mentioned, 11 is the figure which most frequently occurs in the case of all three species, whereas the figures next in order of frequency vary for the different species. Thus in the case of *A. vulgaris*, 10 is far more frequent than 12; with *A. rostrata*, on the other hand, 12 is somewhat, and for *A. japonica* very considerably more frequent than 10. Even in the investigation of small samples this feature is very soon apparent, the characteristic view of each species being revealed at a very early stage of the work. *A. vulgaris* and *A. japonica* differ considerably; to such a degree, indeed, that it is even easier to determine whether a sample belongs to the one or to the other by examining the number of branchiostegal rays than by counting the vertebrae. On the other hand, the difference between *A. rostrata* and *A. japonica* is less pronounceed. There is, however, approximately the same difference between their averages as between those of *A. rostrata* and *A. vulgaris* (0·240 and 0·248 respectively), and the P. F. A. of the two species would most probably fall clear of each other if more accurately determined by investigation of a somewhat larger material than the 83 specimens here employed.

As usual, an attempt was made to discover possible racial differences by examination of three large samples from localities as widely removed as possible (Denmark, England, South of France). From Table IV (1—3) it will be seen, that the investigation of this feature has similarly failed to bring to light any such difference; the variations of the averages as found are independent of the geographical distribution of the samples, that from the south of Europe (10·768) lying between the two from the north (10·807 and 10·745).

Altogether, the result of the present investigation of the number of branchiostegal rays must be stated as follows: it has been found, that specific differences may, by statistical means, be shown to exist, though the variants occurring in each species be the same, or even when the variant most frequently occurring is common to both. The investigations further show, that even very small differences may with perfect certainty be regarded as important, as long as the accuracy with which they are determined is sufficiently great.

With regard to the length at which the full number of branchiostegal rays is present, it may be mentioned that larvae of *A. vulgaris* measuring 38—42 mm. appeared to have the full complement of rays (11 in all).

4. Number of pectoral rays

In Report I, 1913, p. 5—6 mention is made of the investigation as to number of pectoral rays in a couple of samples of older specimens of the European eel, and one sample of an East Indian, short-finned species. No difference could be determined by statistical means between the three samples, which fact is commented on as follows (l. c. p. 7) "From this result we can perhaps conclude, that this character is not suited to the separation of species. When species so distinct have the same number of rays, it is improbable that any difference will exist in this character between the more nearly related European, American, and Japanese eels, but naturally nothing can be said on this point until investigations have been made."

The reason for investigating the East Indian species lay in the fact that there was not sufficient material in the case of *A. rostrata*. Thanks to the frequently mentioned sample of elvers from W. Gloucester, Mass., it has now been possible to include the American eel in the investigations. At the same time, a new investigation of the pectoral rays has been made in the case of the European eel, in addition to which, a small quantity of material consisting of Japanese eels has likewise been dealt with. In the previous investigations, (Report I, 1913) no endeavour was made to consistently compare the pectoral rays from one and the same side of the fish, taking right and left separately, (cf. branchiostegal rays). And as the material previously available for *A. vulgaris* was, in technical respects, not very satisfactory, I have thought it best to make the whole investigation over again.

The work was carried out in the following manner. The right pectoral fin of each specimen was removed and stained with alizarine, cleared in xylol and examined under the microscope. The staining process is frequently attended with some difficulty, especially in the case of young elvers, where the lower rays are often found to be insufficiently coloured. On the other hand, older eels are somewhat difficult to deal with, owing to the necessity of removing the adjacent skin, whereby the pectoral rays may be split lengthwise, occasioning some doubt in the counting. According to my experience, it would seem that fairly old elvers, or especially young eels of 10—20 cm. in length, are best suited to the purpose of investigating the number of pectoral rays, and the present work has also, as far as possible, been carried out with such stages. All the figures have been checked by having the countings twice repeated.

The result will be found in Table V, which is drawn up in the usual manner. We see from this, 1) that *A. vulgaris* and *A. rostrata* differ in regard to the number of pectoral rays, and 2) that no racial difference within either of these two species has been discovered by means of this feature.

Table V. No. of pectoral rays (right side) in *Anguilla vulgaris, A. rostrata* and *A. japonica*

No. of rays	No. of specimens							
	Anguilla vulgaris				Anguilla rostrata			A. japonica
	1 Faxe Bay, Iceland	2 Valentia, Ireland	3 Palermo, Italy	1—3 Total	4 W. Gloucester, Mass., U. S. A.	5 St. Croix; Danish W. Ind.	4—5 Total	6 Kyushyu, S. Japan
21	...	2	1	3	...	...	...	...
20	5	6	3	14	1	...	1	...
19	27	26	27	80	5	1	6	2
18	68	83	64	215	22	5	27	13
17	108	103	91	302	58	23	81	21
16	33	35	46	114	44	16	60	7
15	5	9	5	19	9	5	14	1
14	...	...	...	...	1	...	1	...
Total No. of specimens	246	264	237	747	140	50	190	44
Average No. of rays	**17·382**	**17·409**	**17·316**	**17.371**	**16·79**	**16·62**	**16·74**	**17·18**
σ (Standard deviation)	±0·986	±1·068	±1·044	±1·033	±0·981	±0·880	±0·955	±0·84
P. E. A. (Probable error of average)	±0·0424	±0·0443	±0·0457	±0·0255	±0·056	±0·084	±0·047	±0·086
P. F. A. (Probable fluctuation of average)	17·170—17·594	17.187—17·631	17·088—17·544	17·243—17·499	16·51—17·07	16·20—17·04	16·51—16·97	16·75—17·61

This need not here be further discussed; all that could be said would be but a repetition of what has been stated in considering the figures obtained for the branchiostegal rays.

The supposition advanced in Report I, 1913, to the effect that the number of pectoral rays would be valueless as a character for distinguishing between *A. vulgaris* and *A. rostrata* is thus not found to hold good.

The small amount of material (44 specimens) available for *A. japonica* is hardly sufficient for a fairly accurate determination of the average number of rays for this species, the more so as it consists of young elvers, the pectoral rays of which did not take the stain very well. We find, however, that *A. japonica* occupies an intermediate position between *A. vulgaris* and *A. rostrata*. As to how far its P. F. A. will fall clear of that of the two others, this can only be determined by examination of a greater number of specimens than I have had at my disposal.

With regard to the length at which the full number of rays appears, it may be mentioned that larvae of *A. vulgaris* about 38 mm. long had apparently already their half number of rays, while a specimen 42 mm in length showed 16 rays.

5. Number of caudal rays

The number of caudal rays is the last of the characters to be here dealt with at length. The caudal rays, it is scarcely necessary to state, are those emanating from the last two hypurals. Their number has been found to vary from 8 (a single specimen with 7 should perhaps be regarded as abnormal) to 12. Table VI A shows the total number of caudal rays, whereas in Table VI B, distinction is made between the rays of the last hypural (*d*) and those of the penultimate (*v*).

It will thus be seen, that the number of caudal rays is very nearly identical with that of the branchiostegal rays (cf. Table IV), the range of variation also being the same. There is, however, this essential difference, that the frequency of the separate variants exhibits an entirely different character. If we compare, for instance, the variation for the whole of the *A. vulgaris* material (cf. Table IV A, 1—3 and Table VI A, 1—3) we find that about 50 % of the branchiostegal variants fall to other figures than that of most frequent occurrence, whereas

Table VI A. No. af caudal rays in *Anguilla vulgaris*, *A. rostrata* and *A. japonica*

No. of rays	No. of specimens					
	Anguilla vulgaris				A. rostrata	A. japonica
	1 Nykjøbing, Sealand, Denmark	2 Bristol Channel, England	3 Cette, France	1—3 Total	4 W. Gloucester, Mass., U. S. A.	5 Kyushyu, S. Japan
12	1	1	1	3	2	...
11	35	12	16	63	8	2
10	693	413	530	1636	360	85
9	36	25	34	95	39	2
8	3	3	7	13	4	1
7	...	1	...	1	...	...
Total No. of specimens	768	455	588	1811	413	90
Average No. of rays	**9·9935**	**9·956**	**9·946**	**9·9696**	**9·915**	**9·98**
σ (Standard deviation)	±0·333	±0·367	±0·370	±0·356	±0·4058	±0·299
P. E. A. (Probable error of average)	±0·0081	±0·0116	±0·0103	±0·00564	±0·0135	±0·0213
P. F. A. (Probable fluctuation of average)	9·953—10·034	9·902—10·010	9·897—10.001	9·9414—9·9978	9·848—9·982	9·87—10·09

Table VI B. No. of caudal rays (dorsal and ventral) in *Anguilla vulgaris*, *A. rostrata* and *A. japonica*

No. of rays, dorsal (d) and ventral (v)	No. of specimens				
	Anguilla vulgaris			A. rostrata	A. japonica
d—v	1 Nykjøbing, Sealand, Denmark	2 Bristol Channel, England	3 Cette, France	4 W. Gloucester, Mass., U. S. A.	5 Kyushyu S. Japan
3—6	...	...	...	...	1
4—3	...	1	...	...	...
4—4	1	3	6	5	...
4—5	9	8	8	12	2
4—6	...	...	...	...	1
5—4	23	17	19	23	...
5—5	609	413	442	319	83
5—6	12	4	6	2	...
6—4	...	...	...	1	...
6—5	19	8	8	6	2
6—6	...	1	1	2	...
Total No. of specimens	673	455	490	370	89

in the case of the caudal rays, only about 10 % of the variants lie outside the corresponding figure here. Thus, in spite of the fact that the range of variation is in both cases the same, the number of caudal rays actually varies far less than that of the branchiostegal rays, and is therefore less adapted to the purpose of specific or racial distinction; in other words, it is of less value in classification than the latter. Table VI A further shows, that in spite of the very considerable number of specimens, no characteristic difference between *A. vulgaris* and *A. rostrata* has been revealed; still less, as might be expected, between the different samples of European eels. In all samples the figure 10 is absolutely predominant over all others, and we do not here, as with the branchiostegal and pectoral rays, find that even the investigation of smaller samples quickly furnishes a characteristic view of each species, with a constant order of precedence as regards frequency of the separate variants. It would seem that the average number of rays is lower in the case of *A. rostrata* than for *A. vulgaris*; the difference is, however, so slight as only to be apparent in the second decimal figure. A noticeable peculiarity in the table is the fact that a greater difference may be found to exist between two samples of *A. vulgaris* than between the one of these and the *A. rostrata* sample. From all this it is evident that the number of caudal rays is a feature of little systematic value, and that in any case, a far greater quantity of material would be required in order to demonstrate with certainty a slight difference between the species. Nor does the distinction made in Table VI B between the rays of the last and those of the penultimate hypural seem to indicate any characteristic difference between the species; in addition to which, the material thus drawn up cannot be treated and judged by the usual statistical method.

The caudal rays are present even in very small larvae of *A. vulgaris*. Larvae of less than 2½ cm in length showed as yet no incipient ray formation; this was, however, found to be present in larvae 3 cm long, while the full complement was not apparent until a length of 3½—4 cm was reached.

6. Summary

If we now consider as a whole the results of all the measurements of permanent characters published in Report 1 and in the present work, we arrive at the following general view:

It has proved possible, by means of the permanent characters, to distinguish between the three species, *A. vulgaris*, *A. rostrata*, and *A. japonica*. All the permanent characters investigated have proved to be of importance to the classification, this being, however, only to a lesser degree the case with the caudal rays, the variation of which has been found to be so slight as not to permit of any specific distinction on the basis of the material available.

It has not been found possible to demonstrate, by means of the permanent characters, the existence of "smaller species" or "races" within the separate species; the question has, however, during to lack of adequate material, only been fully investigated in the case of the European eel.

The number of vertebrae is, in general, the most convenient character for separation of the species, in any case, when it is desired to distinguish between the American eel and the other two species[1]. Of 532 specimens of American and European eels, equally mixed, all save only 0.56 % of the total number could be distinguished, with absolute certainty, while in a similar mixed sample of American and Japanese eels, all the specimens could probably have been classified with certainty. Such cases are, however, purely exceptional. As a rule, we find the same variants for the different species, only the distribution of these variants exhibiting any difference. It is therefore necessary, in all other cases, to examine a certain more or less considerable number of specimens before anything can safely be said as to the species to which they belong.

A. rostrata is generally remarkable as having the lowest, *A. japonica* the highest values, while *A. vulgaris* occupies an intermediate position, this being, however, much nearer to *A. japonica* than to *A. rostrata*. A comparison between *A. rostrata* and *A. vulgaris* gives the following:

	Vertebrae	Anal rays	Pectoral rays	Branchiostegal rays
A. rostrata	low	low	low	high
A. vulgaris	high	high	high	low

It is here very remarkable to see, from the above, that *A. rostrata*, which otherwise has everywhere lower figures than *A. vulgaris*, suddenly takes up the reverse position with regard to the branchiostegal rays.

[1] If it is desired to separate samples of *A. vulgaris* and *A. japonica* however, the number of branchiostegal rays, which s far less than that of the vertebrae, is easier to work with.

III. Conclusion

We may now proceed to briefly consider the biological importance of the present variational-statistic investigations as far as concerns the European eel.

The investigations entirely confirm the conclusions at which I arrived in Report I, 1913, to the effect that all European eels belong to one and the same species, within which no constant local races can be shown to exist.

With regard to the variable characters, the following have been examined: 1) ano-dorsal distance, 2) length of head, 3) length of leptocephalus stage (Stage I), 4) length of elver stages (Stages V and VI). The investigations made as to these characters will be dealt with in detail in a subsequent work.

The main results have, however, already been referred to in Report I, 1913; these indicate, that while local differences may be found to occur in European eels as regards most of the above-mentioned variable characters, at any rate at certain stages of developement, these differences do not furnish any means of distinguishing between sub-species or races, owing to the fact that the extremes are connected throughout by gradual stages, in addition to which, the values found are often entirely independent of any definite geographical order.

The permanent characters as treated here are all found to be fully developed, as far as their arithmetical expression is concerned, even in half-grown larvae; the variable characters, however, are of necessity only distinctly marked at later stages of developement in the life of the individual. The larvae which proceed from the spawning grounds in the Atlantic towards the continental slopes of Europe have, even before they approach these waters, all their permanent characters fully formed. The variable characters, on the other hand, do not become marked until after the individuals have penetrated into the waters in which their period of growth is passed, and which differ widely in physical and chemical respects.

This point is worthy of notice, confirming as it does, indirectly, my previous statements (1906—1912) to the effect that all European and North-African eels, whether found on the coasts of the Atlantic, in the Norwegian Sea, the North Sea, the Baltic or the Mediterranean, have their origin in the spawning grounds of the Atlantic Ocean.

We thus find, that the results obtained by biological methods are in excellent agreement with those arrived at by means of the statistical method.

I must in this connection briefly refer to a treatise published in the spring of 1914 by B. Grassi, entitled "Quel che si sa e quel che non si sa intorno alla storia naturale dell'anguilla" (What we know and what we do not know about the natural history of the eel), (Comitato Talassografico Italiano, memoria XXXVII, Venezia 1914).

In this work, as in several previous publications[1]) Grassi attempts to depreciate the importance of some of the results obtained from the investigations made by "Kommissionen for Havundersøgelser" as to the biology

[1] which appeared after I had commenced to publish the results of my investigations in the Mediterranean. These works of Grassi will, in a subsequent paper, be dealt with in chronological order, in order to show what was known as to the biology of the Mediterranean murænoids before the cruises of the "Thor" in 1908—1910, and what was brought to light by the work in question. The material from the Mediterranean cruises of the "Thor" is being dealt with in conjunction with the Atlantic material; the collections are, however, very large (already over 15,000 specimens) and will therefore take some time to thoroughly examine and describe. It should, however, be mentioned, that a survey has already be made of all the larvae available belonging to the two Atlantic species of *Anguilla*.

of the eel and the murænoids generally. These questions have also been treated by reviewers, and I have therefore thought it best to briefly mention GRASSI's statements here.

The writer in question deals with two points of more general interest, viz.:

1) Do the larvae of the eel normally belong to the upper layers? and

2) Does the Mediterranean owe its stock of eels to immigration from the Atlantic?

I have, in my opinion, long since advanced sufficient grounds on which to answer both queries in the affirmative. GRASSI, however, here takes another view, and I have but little hope of being able to convince this well-known zoologist, whose standpoint, as regards investigations in marine biology, is evidently very different from mine. This latter fact, indeed, I take to be the main reason of our disagreement, and it is scarcely likely to be removed until GRASSI has had occasion to form a personal idea of the fishing capacity of the nets when worked by trained men from ships specially equipped for marine investigations, of the conclusions which may then be drawn from comparative hauls, etc. etc.

1) The first question is: At what depth do the larvae of the eel occur? As early as 1906, and later, in 1909, I furnished data sufficient to show that the larvae of the eel normally belong to the upper layers over great depths: the same is also strikingly evidenced by HJORT's investigations with the "Michael Sars" in 1910. The following new data however, may still be mentioned: In the course of the cruise made by "Kommissionen for Havundersøgelser" with the "Margrethe" in the Atlantic in 1913 over 700 specimens of *Leptocephalus brevirostris* were procured. The depths at which these were found will be seen from the following table. It should be added, that only those hauls are recorded which were made at stations where *L. brevirostris* occurred. All the stations in question lie at oceanic depths.

Metres of wire out	No. of specimens (°/₀ of total number)	No. of hauls
from 10 to 110	97.6	104
— 150 - 2000	2.4	39

We might now, I venture to think, reasonably consider this discussion as closed, and refrain from including the sunfish, as to the biology of which opinions are divided. There seems, however, to be but slight hope of this, as long as GRASSI (l. c., p. 14) can attempt to explain the fact noted by HJORT and myself, that the eel larvae are exclusively or chiefly taken in the upper layers, by suggestions like this: "... at greater depths, the conditions of life may perhaps be more favourable for the larvae, thus rendering them better able to avoid capture"![1])

GRASSI has made some investigations in the course of a few short cruises on board the warship "Ciclope" round about the Straits of Messina, and there found 4—5 larvae, which may have been taken at 50, 200, 400 metres depth or perhaps nearer the surface. This, however, is nothing new; my earlier publications contain numbers of similar instances. The point at issue is, whether the great majority of the larvae are to be found near the surface, and this I consider as having long since been finally demonstrated to be the case.

2) The second question is the origin of the Mediterranean stock of eels. As to this, GRASSI observes (l. c., p. 30) "Schmidt's hypothesis, that the eel does not spawn in the Mediterranean, is not, at present, sufficiently proved" and again (l. c. p. 17) "the further I pursue my investigations the more I become convinced that the eel must spawn in the Mediterranean".

My contribution to the elucidation of the question consisted of two series of investigations, viz. 1) biological and 2) a study of specimens of eels from the two areas.

Among GRASSI's arguments ad (1) the following may be mentioned:

[1] The *Cyclothone*-species, and many other species were, on our cruises, regularly taken only in the deepest hauls, where *Leptocephali* were not found. This fact we should then, according to GRASSI, presumably be able to explain by the theory that the *Cyclothone* is in reality a surface fish, but finding better conditions of life near the surface, would there be better able to avoid capture than in the deeper layers!

My measurements of eel larvae had shown, that the size of the larvae increased from Gibraltar eastwards in the Mediterranean: I found, that of larvae below 70 mm, there were about 60% at Gibraltar; somewhat farther to the east only about 5%, and near Messina only about 3 %. As against this, Grassi states (l. c. p. 13) that he once, in March 1895, in examining a large sample from Messina, found no less than 89 % of specimens below 70 mm (average 64·34 mm). Here, however, I may observe, that both my own measurements of material collected at Messina during a period of 14 months[1], and Grassi's later measurements (l. c. pp. 34—37) indicate, that the conditions in regard to size as stated by me are the rule, and Grassi's find in March 1895 the exception. The occasional appearance, especially in the spring, of larvae somewhat below the usual size as far east as Messina is in no way remarkable; the immigration from the spawning grounds in the Atlantic, dependent as it is upon variations of currents, etc., can of course take place with greater or less rapidity. Here again, the rule is the main point, and the rule is, that the Messina larvae are large, and that neither Grassi nor I have succeeded, despite all our efforts, in obtaining a single specimen as small as those which regularly occur throughout certain large tracts of the Atlantic. (The smallest of several thousand known specimens from the Mediterranean measures 51 mm).

I repeat, therefore, what I asserted in 1912, that the reason why these growing stages were easily discovered in the Atlantic, but not, despite my continued efforts, in the Mediterranean — and it should be remembered, that one of the main objects of the "Thor"'s Mediterranean cruises was to make particular search for these younger stages — is purely and simply this, that they do not exist in the Mediterranean, because the eel does not spawn in that sea. I maintain, therefore, that I have already, in 1912, furnished adequate proof of the correctness of my assertion. In addition, I may here quote some figures from the cruise of the "Margrethe" in 1913. In the course of this cruise, during which investigations were more particularly made farther to the west and south than on the previous voyages of the "Thor" in the Atlantic, over 700 larvae of the European eel were, as previously mentioned, found. Of these, 95 % were less than 50 mm long, and 54 % below 40 mm!

Whatever scepticism may hitherto have existed with regard to the justification of my assertion as to the origin of the Mediterranean eel, these figures compared with the figures obtained during the Mediterranean cruises, leave, it would seem, no longer any grounds for refusing to accept the same.

That we found, in the course of our comparative investigations, fewer eel larvae in the Mediterranean (cf. Grassi, l. c., p. 15) than in the Atlantic, is primarily due to the fact that fewer exist there than in the latter, which again is a natural consequence of the fact that the Mediterranean larvae originate from the Atlantic. By making further hauls at those places in the Mediterranean where we found the larvae, it would have been easy to procure a greater amount of material. As, however, the larvae were of the same size as those which may easily be procured at Messina, it would scarcely have been justifiable to so employ the services of the steamer, and of an expedition equipped for the purpose of procuring a comprehensive view of Mediterranean conditions.

Grassi refers (l. c., pp. 16—17) to some investigations which he has commenced with a view to demonstrating the differences between eels from various localities. He has observed, that the last hypural of the elver usually exhibits a longitudinal fissure, which may be long ("profondamente fesso") or short ("limitamente fesso"), or entirely lacking ("intiero"). Calculating the percentages of individuals in a sample having long fissures in the last hypural, he finds, apparently, a somewhat higher percentage among samples from the Atlantic, the Adriatic, and certain parts of the Tyrrhenian Sea than in samples from another portion of the last-named water

[1] From 1. March 1911 to end of May 1912, and further, from Sept. 1912 to 7 Jan. 1913. A sample from May—June 1911, containing 97 specimens, showed an average length of 75·79 mm, another from July—Aug. 1911, of 155 specimens (the latter taken from the stomach of a sunfish), averaged 75·35. The other samples exhibited approximately the same conditions as to size, without regard to the season of the year.

(Pisa and Leghorn). The investigations have not, however, been completed, and the figures as given indicate nothing beyond the fact that he has not succeeded in demonstrating any constancy for one and the same locality. Now it happens, that we have in our material elvers from two of the places which Grassi has here included, viz. Leghorn in Italy, and the river Severn in England. He gives the figures for Leghorn as 53.5 % and for the Severn as 66.4 % of long-fissured individuals. On examination of 104 and 114 specimens from Leghorn and the Severn, cand. mag. Strubberg obtained the following results:

	Leghorn	Severn
No fissure	10 %	17 %
Short --	16 %	21 %
Long --	74 %	62 %

or very nearly the opposite of Grassi's.

The fissure referred to is formed, as examination of young larvae has shown, by two parts fusing together, and cases exist where no fissure, but only a line, is apparent. And it will in any case not infrequently be a matter of judgement as to how a particular specimen should be classified. This "character", can therefore only be employed with the greatest caution. As Mazzarelli has emphatically pointed out (Note critiche sulla biologia dell' Anguilla; Rivista di Pesca e Idrobiologia, 1914, No. 2, p. 52), it is only by using the statistical method ("valendosi del metodo statistico") that we can hope to demonstrate with any certainty the existence of different races. This method cannot, however, be employed in the form in which Grassi has framed his investigations; it would for instance be necessary to actually measure the proportionate length of the fissure as compared with that of the hypural itself in order to render the character available for statistical investigations. This has not been done, and Grassi does not, indeed, draw any conclusions from the investigation, but merely observes that "by continuing the investigations and extending them so as to embrace other characters, it may perhaps be possible to demonstrate the existence of a difference between the Mediterranean and Atlantic eels". — As to this, it may be mentioned that the investigations by means of variation statistics referred to in the present work show, that this supposition has not been confirmed.

Finally, therefore, I consider myself justified in asserting, that Grassi[1]) has advanced nothing which can in any way affect the conclusions I have drawn as to the origin of the Mediterranean eels on the basis of the investigations carried out under my supervision.

[1] I take the opportunity of pointing out that Grassi in certain cases seems to have overlooked the fact that the results which he has obtained from investigations of *Leptocephali* and elvers have already been published by Danish writers. Thus for instance, Grassi states (l. c. p. 17, note) "My latest investigations show, that the Mediterranean elvers are shorter than those from the Atlantic". The same fact is noted, in a somewhat more correct form, in my frequently mentioned Report I, 1913, p. 23, and is also evident from measurements published by me in 1911 in the "Fischerbote" (see also Orsenigo 1911). — Grassi further states (l. c. p. 19, and 1913, p. 107) that the reduction in length which takes place during metamorphosis amounts, or can amount, to about 1 cm, a point which I had set forth in detail as early as 1909 (Meddelelser fra Kommissionen for Havundersøgelser, Serie Fiskeri, Vol. III, No. 3, 1909, p. 7.) And in the last-named periodical, Serie Fiskeri, Vol. IV, No. 3, 1913, A. Strubberg has explained at length the development of the pigment during the metamorphosis of the elvers, and furnished illustrations of the same. Grassi (l. c.) treats the same subject, and his illustrations (on Plate III) correspond exactly to Strubberg's; he makes, however, no mention at all of this writer's work.

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