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MICHOACAN ICHTHYOLOGY IV
CONTRIBUTION TO THE BIOLOGY AND SYSTEMATICS OF THE LAMPREYS OF JACONA, MICH., MEXICO

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ABSTRACT

In 1887, T.H. Bean described a petromyzont which he called *Lampetra spadicea*, based on a single specimen sent him from Guanajuato. In the Spanish translation of Bean's work published in 1892, Dugès assigned the common name "Jacona eel" to the species, clearly indicating its origin and type locality. Little attention has been given to this member of the Petromyzonidae since those early accounts.

*Numbers in the right-hand margin indicate the corresponding pages in the original.

As there were only six known specimens of Lampetra spadicea (three in the United States National Museum and three at the University of Guanajuato Museum), 1354 ammocoetes and approximately 100 adults were captured and studied in Jacona and Zamora in the state of Michoacán and in Chapala Lake in Jalisco (see "Material and Methods").

Tetrapleurodon Creazer and Hubbs 1922, the genus to which the Jacona lamprey is currently assigned, differs from Lampetra and Entosphenus.

Some specimens captured were of a hitherto unknown dwarf form, introduced and described here under the name of Tetrapleurodon geminis. Variations in specific characters and a comparison with T. spadiceus show that growth of the particular features which distinguish the two species is isogonic and that, accordingly, such relative size data can serve to separate one species from the other.

Since the larvae of the two species are indistinguishable, the description given in these pages is common to both, from a morphological point of view and in terms of the information provided on growth, feeding habits and other general biological features.

The ammocoetes hatch in the Celio River in Jacona, Mich. and probably in other as-yet unidentified areas of the basin, between the month of November and the following January. After growing for three years they undergo metamorphosis. Following a very short migration, T. geminis spawns and dies, while T. spadiceus migrates, after transformation, to Chapala Lake or the larger rivers of the Lerma drainage system. After two years of continuous growth, the latter species returns to the spawning grounds, mates and dies.

Ammocoete length shrinks during the rainy season, particularly in individuals of the first year class.

Sexual dimorphism is noted in the adults of both species. Fecundity is higher in T. geminis.

INTRODUCTION 108

Petromyzonts are cyclostomes which live in both fresh and salt water. Once the marine species and those which inhabit lakes or large, swift rivers such as the Mississippi or the Danube reach sexual maturity, they seek clear water stretches upriver, relatively close to the source of the stream. Here, after courting, males and females empty their gonads, the eggs are fertilized externally, and the parents die.

The hatched larvae, known as ammoecotes, bury themselves in the soft river bed of silt, sand and organic matter.

After a larval stage lasting several years, the ammocoete undergoes radical metamorphosis, and the transformed organism retraces the path taken by its parents. It now feeds on the blood of fishes, to which it attaches itself using a suctorial oral disk. The tongue, equipped with horny teeth, tears into the tissues of the host and sucks out the blood. At sexual maturity the gonads, particularly in females, fill practically the entire abdominal cavity, flattening the intestine, so mature lampreys cease to eat and begin their spawning migration to clear-water streams.

Some species spend their entire lives in lakes and rivers, never reaching the sea. Two very similar forms are often found to share the same area: after metamorphosis, one species reaches sexual maturity immediately, ceases eating and dies shortly after spawning, smaller at death than at the end of the larval phase. The other species feeds on blood after metamorphosis and continues to grow until it is sexually mature, some two or more years later. Naturally, the blood-eating individuals grow much larger than those which reach sexual maturity early.

The general consensus of ichthyologists today is that each of these forms represents a different species. Based on evidence unearthed by us and described under "Systematics", we will assume in this work that different taxa are involved. This is supported by the fact that our captures yielded specimens both of lampreys that feed on the blood of fishes after metamorphosis and those which reproduce shortly after transformation and then die.

In order to avoid terms like "parasitic", "hematophagous", "non-parasitic", "praecox", and others that have been used to designate classes, forms or types of lamprey, we will use "*marinus*-type" to refer to those with a biological cycle comparable to that of *Petromyzon marinus*, and "*planeri*-type" for lampreys which do not eat at the adult stage and thus resemble *Lampetra planeri* Bloch.

Although the Jacona lamprey was described more than seventy years ago, no information has been available on its living conditions, development or life cycle generally. Furthermore, the existence of a *planeri*-type 109
counterpart was unknown.

In 1887 T.H. Bean described a species of petromyzont which he called *Lampetra spadicea*, based on an adult specimen sent by Dr. A. Dugès to the United States National Museum in Washington, D.C. and, in the author's opinion, originating in Guanajuatan rivers. Bean had also handled a larva specimen received earlier from Dr. Dugès; although the original description does not mention the larval stage, Plate XX. Fig. 6 gives a diagrammatic representation of a larva in longitudinal section and a sketch of the animal's oral disk.

Several years later, in 1892, *La Naturaleza*, journal of the former Mexican Natural History Society, published Bean's description of *Lampetra spadicea* translated into Spanish by Dugès, who added a note on coloration and gave the animal the common name "Jacona eel".

Subsequent authors have done little more than recopy Bean's data. Only Meek (1904) contributed information on the Chapala species, based on specimens captured by Nelson, but provided no data on collection date, number of animals in the sample or new features of the species.

BACKGROUND: Although *Petromyzon marinus* is a Linnaean species, little research has been done on lampreys, and most of it is relatively recent. Dumeril called the larva of this animal *Ammocoetes* in 1817, and a scant year later LeSueur was describing a new species on the Massachusetts coast, *Ammocoetes bicolor*, which is simply a synonym of *P. marinus*. Anywhere from sixteen to nineteen species are currently referred to the family Petromyzonidae, there being some debate over the validity of several of them.

Müller (1856) measured six lamprey larvae, probably from *Lampetra planeri*, but did no subsequent studies on growth. Lubosch (1903) and Loman (1912) were the first to speculate on the age and growth of ammocoetes, after their study of numerous specimens of the aforementioned species. While Müller assumed *a priori* that his 6 cm specimens were just over one year old and those 14-16 cm long were approximately two years old, the other authors mentioned formed "year classes" with material from one or two hauls only, and deduced that the larval phase lasted from four to five years.

In the U.S.A., Schaffner (1902) studied age and growth of *Entosphenus appendix* larvae in specimens captured near Ann Arbor, Michigan. Like the researchers referred to above, he formed year classes using material from a single capture and calculated age and growth of the species based on the mean values for each class. Twenty years later, Okkelberg (1922) described his research into the growth and life cycle of *Ichthyomyzon unicolor*, based on material from several collections in the Thunder Bay River, Michigan (U.S.A.). This author prepared seven-year growth curves and calculated size increases based solely on the value for each angle of the graph, i.e., mean growth, observed and divided by the number of specimens (so-called "additive" or "arithmetic" ammocoete growth). 110

The most complete account to date of larval growth in lampreys appeared in 1930. From his work with Lampetra planeri, L.P. Schultz produced length frequency distributions for ammocoetes captured near Seattle, Washington, and subjected his data to standard statistical analysis procedures. He notes that no weight-length ratio is presented for the individuals examined because water content can lead to serious errors of interpretation, especially in smaller specimens. Some of Schultz's deductions are that the larval stage in this species lasts for four years, that its behaviour resembles that of E. appendix and I. fossor, that it does not feed on blood and that all individuals die after reproducing.

Little attention has been given to other growth-related aspects of post-embryonic development in lampreys. The earliest work in this area is probably that of Yarrel (1831), who reported having observed the spawning of Petromyzon marinus. Ferry (1882) conducted several experiments on fertilization and incubation in the same species. Gage (1893) studied some stages of the species' sexual behaviour and affirmed - probably for the first time - that the adults die after mating, without ever returning to the sea. Other authors (Egli, Burrough, etc.) have confirmed this same behaviour after examining breeding and dead specimens.

Some of the earliest and most detailed works on the topic are the publications of Crotonei (1922 and 1924) on the biology of Petromyzon marinus and Petromyzon fluviatilis, based on experiments and extensive observation. The total length of adult specimens kept in aquariums was measured over a period of two to three months, both at the onset of the experiment and as each lamprey died. From these observations, Crotonei deduced the existence of the shrinkage phenomenon, or decrease in total length of these animals when they reach sexual maturity.

This same author reports his work and findings on the atrophy of the intestine in the wake of metamorphosis in *P. planeri*, which spends its entire life in fresh water, unlike *P. marinus* and *P. fluviatilis* which embark on a second growth period after transformation.

In the introduction to his account (1924), Crotonei laments the dearth of literature on the biology of *P. marinus*, particularly data on its migration and larval phases. He also provides studies of the systematic characters of the petromyzonts mentioned.

The atrophy of the lamprey gut during the reproduction phase has also been examined by Gage (*op.cit.*) and Weissenberg (1925). The latter reported successful interspecific fertilization of *P. fluviatilis* and *P. planeri*, but no mention is made of how long the offspring survived.

In their review of the systematics of the holarctic lampreys, Creaser and Hubbs (1922) and Berg (1931) describe some features of the habits of
each species referred to in their publications. According to Berg, very 111
little was known about lampreys at the time; major contributors to date in his view were Crotonei, Gage, Weissenberg, and Creaser and Hubbs.

There is a similar dearth of information on lamprey fecundity. Studies by Surfase (1899), Gage (1928) and Leach (1940), while not in-depth efforts, are the only real antecedents of the work of Vladykov (1951), who contributes information on fecundity in I. fossor, P. marinus, E. lamottenii and I. unicuspis.

Vladykov is also the author of many important studies on the lampreys of Canada, centring primarily on systematics.

At least 200 publications were consulted in the preparation of this article, but all of the contributions to the knowledge of petromyzonts found are of secondary importance for our research, the majority being taxonomic studies involving species in distant regions of the world.

Finally, we should mention G. Zanandrea's work on European petromyzonts, which provided valuable data for an understanding of the biology of the group generally.

A table devised by Zanandrea distinguishes between "parasitic" and "non-parasitic" species and outlines the general characters of each form.

As no information whatever is available on the biology of the Jacona lamprey, we believe that this contribution to the knowledge of that species will serve a useful purpose. Specifically in terms of post-embryonic development and characteristics of the species, some of the facts recorded, such as shrinkage in length in the first year of larval life, post-metamorphic migration of the new species described here, and other secondary information, were unavailable previously for this or any other lamprey.

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MATERIAL AND METHODS

FIELD WORK. Only six specimens of T. spadiceus were known to exist,
three in the United States National Museum (types described by Bean in 1887) 112
and three never studied, in the A. Dugès Museum at Mexico's University of Guanajuato. Our first step was thus to obtain sufficient material for the research to be undertaken.

Despite sporadic capture attempts over a 15-year period in the region, it was not until April of 1961 that we obtained our first Jacona lamprey specimen in Chapala Lake, followed on August 8 of that same year by another adult specimen taken from the Duero River in Zamora, state of Michoacán.

FIG. 1. Banks of the Celio River, Las Vegas estate, Jacona, Mich., where ammocoetes described in this study were collected.

A first search in the Zamora and Jacona region in September of 1961 failed to produce any larvae, even in the Celio River, which would later yield all the ammocoetes used in our research.

After a number of equally unsuccessful attempts to locate either larva or adult specimens, all of them involving lengthy and careful exploration of potential capture sites, 12 minute larvae were finally discovered in Jacona, Mich. on January 5, 1962. Subsequent collection efforts were much more fruitful.

On November 18, 1962, after adult lampreys apparently engaged in mating activity were observed in the Celio River in Jacona, Mich., some five litres of mud containing minute larvae were dredged up and fixed in formalin; at the National School of Biological Sciences, researchers found the mud to 113
contain numerous eggs, probably of Tetrapleurodon.

A breakdown is given below of larva captures on the banks of the Celio River in Jacona, Mich., primarily at the spot known as "Quinta Las Vegas". The specimens were obtained from a large quantity of mud screened through 0.25 cm mesh.

1962	Number
January 6	28
March 11	76
May 22	82
August 5	25
August 20	122
October 27	36
November 18	85
1963	
January 13	145
April 15	216
July 15	107
September 27	122
October 12	104
November 10	187

All larvae were collected within a 300 m radius of the same site, in order to eliminate or attenuate the influence of local growth factors: Zanandrea (1961: 523) has noted that ammocoete length and weight vary in different streams and at times in different parts of the same stream, while Okkelberg (1922: 9) found growth differences in Ichthyomyzon unicolor larvae taken from sites 185 miles apart.

A total of 78 adult or transformed individuals were examined. Eight came from Chapala Lake in Jalisco, 31 were captured at breeding grounds in Jacona, Mich., and the remainder were collected by fishermen who found them attached to carp and catfish trapped in the Duero River. The following table shows the material gathered at each site on each date:

114

Date	Site	Number
1961		
April	Jocotepec, Chapala Lake, Jal.	1
August 8	Zamora, Mich.	1
September	" "	1
October 7	" "	1
October 14	" "	2
October 19	" "	1
October 21	" "	18
November 15	" "	2
November 27	" "	1
1962		
January 5	Jacona, Mich.	13
April	Zamora, Mich.	2
May 24	" "	1
July	Chapala, Jal.	7
June-July	Zamora, Mich.	7
July 10	" "	1
July 23	" "	1
November 19	Jacona, Mich.	18

COUNTS AND MEASUREMENTS: Both larva and adult specimens were fixed in a 4-6% formalin solution immediately after they were captured, and later preserved in the laboratory in 70% alcohol.

The total length of each specimen was measured. Lengths of the smaller individuals, captured in November and January, were estimated to the nearest tenth of a millimetre, while medium-sized and larger specimens were measured to the nearest millimetre.

Standard measurements used in cyclostome research to date were taken in all post-metamorphic and larger larvae. Generally speaking, we followed the procedures set out by Regan (1911), Creaser and Hubbs (1922), Berg (1931 and 1932), Hubbs and Trautman (1937) and Vladykov (1949).

The following lengths, shown in Figure 2, were measured:

Total length, from the extreme anterior edge of the oral disk to the tip of the caudal fin.

Prebranchial length, from the extreme anterior point of the oral disk 115
to the anterior edge of the first gill opening.

Branchial length, from the anterior edge of the first gill opening to the posterior border of the last cleft.

Trunk length, from the posterior edge of the last gill opening to the cloaca.

Tail length, from cloaca to tip of caudal fin.

Postorbital length, between posterior edge of the eye and anterior border of first gill opening.

Orbital, horizontal diameter of the visible eye.

Oral, anteroposterior length of the oral disk, pressed until the lateral edges meet and entire disk resembles a groove or cleft.

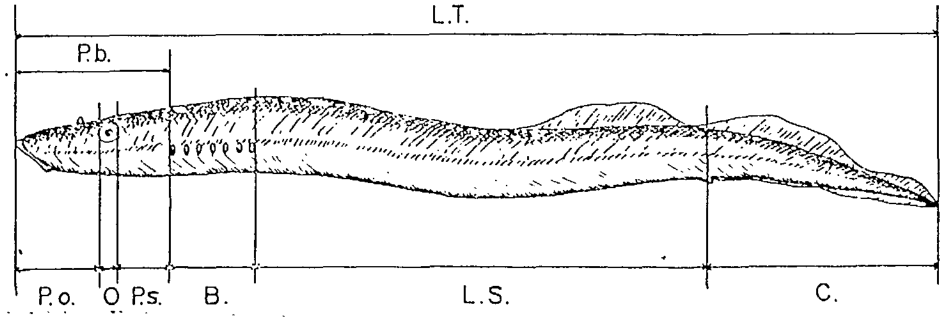


FIG. 2 Body proportions measured in specimens. B - Branchial length. C - Tail length. L.T. - Total length. L.S. - Trunk length. O - Orbital length. P.b. - Prebranchial length. P.o. - Preorbital length. P.s. - Postocular length.

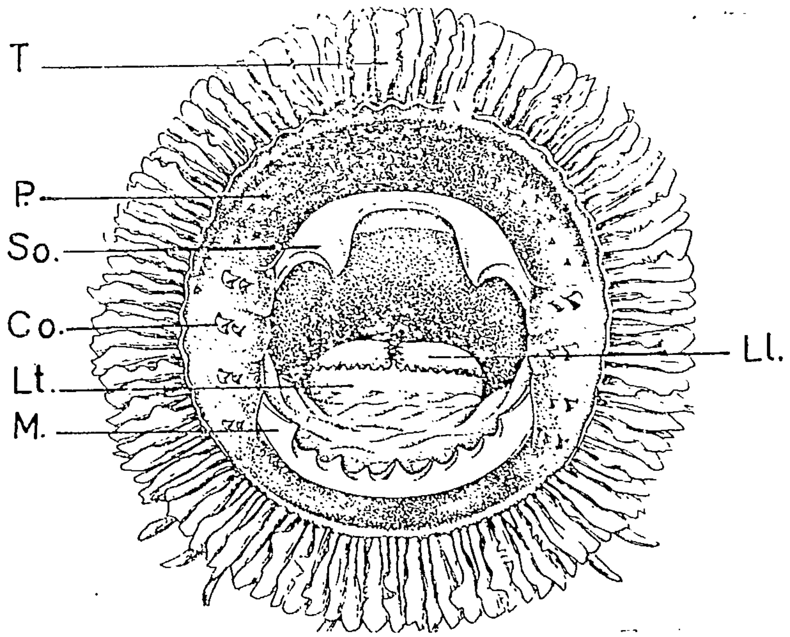


FIG. 3 Oral funnel of Tetrapleurodon. Co - Circumoral teeth. Ll - Longitudinal lingual lamina. Lt - Transverse lingual lamina. M - Infraoral lamina. P - Oral disk teeth. So - Supraoral lamina. T - Oral tentacles

The myotomes from the last gill opening to the cloaca were counted, as 116
were the teeth on the transverse lingual lamina, the circumoral "teeth" and cusps present in each, and the large and small cusps on both supraoral and infraoral laminae (see Figure 3).

Measurements to the nearest tenth of a millimetre were converted to relative size data, by dividing prebranchial, branchial, trunk and tail lengths by the total taken as as a standard, and postorbital, orbital, preorbital and oral lengths by the prebranchial, expressed as thousandths.

Since some authors use branchial length as a standard for calculations of relative values of small measurements, the preorbital, orbital and postorbital length were calculated.

The standard deviation of the values obtained in each case was calculated, multiplied by two, summed and subtracted from the mean, to test whether the results represented more or less than 95% of the hypothetical population.

Calculations for each character commonly used to differentiate species of Petromyzonidae were done separately for metamorphosed specimens of the marinus type and those of the planeri type. Minimum, mean and maximum values were noted as was the standard deviation referred to above. Also calculated for every character corresponding to both types were the statistical significance of the difference between the means and the probability of the two groups belonging to the same population.

The values for "P" of some characters were found to be less than 0.05. However, it was decided that since groups of individuals of differing lengths were being compared, with one group containing specimens larger than those in the other group, the differences could be due to allometric growth, involving as they do relative body proportions, for which the standard used was total or branchial length of each specimen.

To address this question the allometric coefficient "k" was calculated using the formula suggested by Simpson and Roe (1939):

$$k = \frac{\Sigma(\log dx \cdot \log dy)}{\Sigma(\log dx)^2}$$

where "dx" is the deviation of the logarithms of the values for the standard size selected and "dy" is the deviation of the logarithms for measurements of the part of the organism being valued relative to that standard.

For example, the allometric coefficient "k" for total length (x) and 117
branchial length (y), in a group of Tetrapleurodon which included both large and small specimens, was calculated as follows:

X	Y	LOG X	LOG Y	DX	DY	DXDY	$(DX)^2$
113	10.5	2.0530	1.0212	−0.2640	−0.2640	0.0697	0.0697
127	12.7	2.1038	1.1038	−0.2132	−0.1814	0.0387	0.0455
187	19.0	2.2718	1.2787	−0.0452	−0.0068	0.0003	0.0020
197	19.0	2.2845	1.2787	−0.0225	0.0068	−0.0001	0.0005
200	17.8	2.3010	1.2504	−0.0160	−0.0348	0.0005	0.0003
217	23.0	2.3765	1.3075	0.0595	0.0223	0.0013	0.0035
240	20.0	2.3802	1.3010	0.0632	0.0158	0.0010	0.0040
261	25.2	2.4156	1.4014	0.0996	0.1162	0.0116	0.0099
305	28.0	2.4843	1.4472	0.1673	0.1620	0.0271	0.0280
308	29.0	2.4885	1.4624	0.1715	0.1772	0.0303	0.0123
		23.1702	12.8523			0.1804	0.1757

x = total length dx = deviation log x
y = branchial length dy = deviation log y

Sum of dx.dy = 0.1804

$$k = \frac{0.1804}{0.1755} = 1.02$$

Sum of $(dx)^2$ = 0.1757

Growth is considered to be isogonic when the value of "k" equals or is very close to unity, as is the case here.

Both metamorphosed individuals and larvae more than 100 mm long were examined internally to record sex, gonad development, digestive tract, filtration apparatus and endostyle of the ammocoetes.

Twenty transformed specimens and about the same number of larvae were completely dissected in order to study their internal structures.

Estimates were made of the number of eggs in the ovaries of eight mature females, five of them *marinus*-type and three *planeri*. The complete ovary of each specimen was weighed and then a small portion of each. The ovules in the smaller portion were counted carefully and the number obtained was divided by the weight of the piece in grams in order to obtain egg numbers per gram and a very rough estimate of the ovules in the whole ovary. The procedure was repeated in three specimens using different portions of the ovary, and the results were averaged. This step was not followed for the remaining individuals because the results recorded for each of the first three specimens were very similar.

The total number of ovules in the ovary was then divided by the specimen's weight in grams to determine relative fecundity.

Using a dissection lens and placing the edge of one slide on another, eggs were placed in a continuous straight line. The length of each string
was measured and divided by the number of ovules, to obtain the approximate 118
diameter of the eggs in millimetres.

The lengths of the larvae captured in each haul were then plotted, using constant class intervals of 10 mm.

To chart growth, the time in months was marked on the abscissa of a system of Cartesian coordinates and the length of the individuals on the ordinate. Vertical lines recorded the range of variation encountered in each sample. The arithmetic mean was noted in each case.

Since the two and three year old larvae captured in a given group were virtually indistinguishable in terms of length, their gonadal development was carefully noted. For all practical purposes, it was decided that specimens showing no indication of gonad development were in their second year and those with visible genital organs or some evidence of development were three years old, no matter what their actual length. Obviously, specimens showing clear signs of metamorphosis were assigned to the second group.

The resulting growth curve was then fitted as follows: the values corresponding to the two January captures the first year were added and averaged; they were treated as a single group, since there was only seven days difference between them. Next, the mean of each class was taken, and finally, at the end of the curve, based on the figure for May in the second year, three-point running means were calculated to smooth the curve.

Using the new curve values, the geometric growth index corresponding to the increase or decrease in mean total length was calculated for each of the periods elapsed between adjacent values on the curve.

The following formula was used to calculate the exponent of geometric growth

$$G = \frac{\log Y_o - \log Y_t}{t} \cdot \frac{1}{0.434294}$$

where G is the geometric growth index, Y_o the value of mean length at the beginning of a period, Y_t that same value at the end of a period, and t the number of days elapsed. The second factor, in the form of a fraction, is the inverse of "e", the base of the natural logarithm system.

SYSTEMATICS

In their 1922 review of the holarctic lampreys, C. W. Creaser and C. L. Hubbs referred the species then known as *Lampetra spadicea* Bean. to the genus *Entosphenus* and created a new subgenus, *Tetrapleurodon*, to hold 119
that single taxon.

In 1930, Jordan, Evermann and Clark elevated *Tetrapleurodon* to the rank of genus, and L. S. Berg (1931) returned the species to *Lampetra*.

An examination of the material set out thus far in our study appears to support the views of Jordan . Evermann and Clark (1930) and Vladykov (in lit.), considering *Tetrapleurodon* as a valid genus, assigned to it the Jacona lamprey, broadening its description as follows:

Gen. TETRAPLEURODON Creaser and Hubbs

TYPE SPECIES: Lampetra spadicea Bean 1887.

Freshwater Petromyzonidae which never reach the sea during migration. Anterior labial teeth few, non-pavemental, not forming radial series, but tending towards a concentric circular serial arrangement. Supraoral lamina, generally with only two cusps, known as the primary cusps. Typically one series of small external labial teeth and another in the infralabial region. Nearly straight-edged transverse lingual lamina, with 17-22 minute cusps, the central one slightly enlarged. Infraoral lamina with 5-9 cusps: 5 large alternating with 1-4 smaller ones.

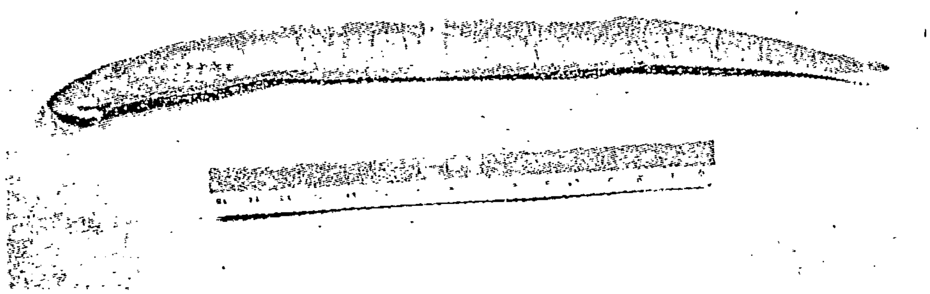


FIG. 4 Tetrapleurodon spadiceus (Bean).

Maximum total length recorded: 30-31 cm

Differs from nearest genera Entosphenus and Lampetra in following characters: supralabial teeth of Entosphenus show no tendency to form concentric series; uniformly strong median cusp on supraoral lamina; second

and third lateral circumorals always three-cusped; no outer labial teeth. 120
Lampetra has very few supralabial denticles, no supplementary cusps on the supraoral lamina, three circumorals only (median tricuspid, end teeth bicuspid), no outer labials or infralabials; median cusp of transverse lingual lamina enlarged.

DISTRIBUTION: Duero River in Michoacán and affluents; Chapala Lake and Lerma River in states of Jalisco and Michoacán.

SPECIES: Two. *T. spadiceus*, a *marinus*-type species, and another of the *planeri* type, described here as a new species.

Tetrapleurodon spadiceus (Bean)

Lampetra spadicea Bean. 1887: 374. Bean 1892: 283. Dugès 1892: 171. Eigenmann 1893: 54. Jordan and Evermann 1896: 13. Herrera 1896: 7. Meek 1904: 2. Regan 1908: 184. Eigenmann 1909: 303. Eigenmann 1910: 376. Alvarez 1950: 19.

Entosphenus (*Tetrapleurodon*) *spadiceus* Creaser and Hubbs 1922: 10.

Tetrapleurodon spadiceus Jordan, Evermann and Clark 1930: 9. De Buen 1940b: 4. De Buen 1946: 263. De Buen 1947: 108. Alvarez and Cortés 1962: 99.

DESCRIPTION: Based on 54 specimens captured in Jacona and Zamora, Mich., and in Chapala Lake.

Marinus-type lampreys, middle size range within the family; the longest individuals studied measure 31 cm overall. After metamorphosis, during which total length shrinks, growth resumes, so adults are always longer than larvae.

From 60 to 65 myotomes, typically 62-64, counted from posterior edge of last gill opening to anterior border of cloaca. Transverse lingual lamina with 17 to 22 teeth. Lateral circumorals four, generally bicusps; five on one side were recorded once, and three once. Supraoral lamina with two primary cusps; rarely, one intermediate secondary cusp and even more rarely, two.

Prebranchial length contained 6.5 to 9 times in total length, branchial 9 to 15 times. Trunk length, half of total or less. Tail length contained 3.5 to 4.5 times in total; preorbital 1.7 to 2.1 in prebranchial. Eye diameter 7 to 8.5 times, postorbital 3.5 to 5 times and oral 1.7 to 2.3 times in prebranchial length.

VARIATION: Table 1 shows the minima, means and maxima for the body proportions of this species, to show the variation encountered. Values for meristic characters are as follows: Secondary cusps on the supraoral lamina, in addition to the two primary cusps: none in 55 specimens, one in 12, and two in two; an examination of 48 individuals revealed 39 with four bicusp circumorals on each side, one individual with five bicusps on one
side and four on the other, three specimens with one tricusp, and five in 121
which one side of the mouth contained only three bicusps. Variation in cusps on infraoral lamina (first figure refers to large cusps, second to

smaller cusps, and number in brackets to frequency): 4 - 3(1), 4 - 4(1), 5 - 0(8), 5 - 1(3), 5 - 2(8), 5 - 3(8), 5 - 4(21). Myotomes: 60(3), 61(6), 62(6), 63(18), 64(10), 65(6).

TYPE LOCALITY: Jacona, Michoacán, Mexico.

We can infer from Dugès' use of the term "Jacona eel" for Lampetra spadicea Bean. that the species' type locality is Jacona, state of Michoacán, and not the rivers of Guanajuato, since Dugès was well aware of the origin of the specimens. Furthermore, waterfalls between Chapala Lake and the part of the basin which drains the state of Guanajuato appear to be an insurmountable obstacle for lampreys attempting to negotiate them during spawning migration.

Tetrapleurodon geminis sp.nov.

HOLOTYPE: A male specimen 136 mm in total length, captured at Jacona, Mich., Mexico on January 3, 1962 by J. Alvarez and Mauricio J. Ocampo.

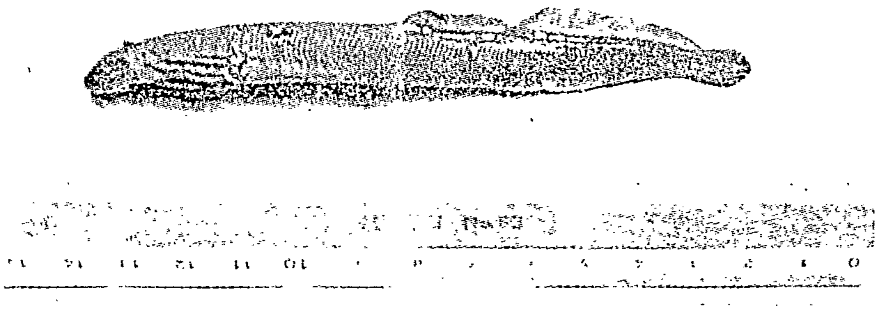


FIG. 5 <u>Tetrapleurodon geminis</u> sp.nov.

HOLOTYPE MEASUREMENTS (in mm): Prebranchial length 17.2, branchial 14.5, trunk 59.3, tail 42.2, postorbital 4.2, orbital 2.7, oral 7.8, preorbital 11.0, predorsal 63.6. The specimen has 62 myotomes, 19 teeth on the transverse lingual lamina; four circumorals on the right side, the superior two unicuspid and the inferior two bicuspid; only three unicusps on the left side.

PARATYPES: 12 specimens captured contemporaneously with the holotype and 9 collected at the same site by J. Alvarez on November 19, 1962.

DESCRIPTION: Small lampreys, maximum recorded total length 142.5 mm; 122
consistently smaller than the largest larvae. From 60 to 65 myotomes, typically 62 to 64, counted from posterior edge of last gill opening to anterior border of cloaca. Transverse lingual lamina often not well developed. Some circumorals rudimentary or absent. No supplementary cusps found on supraoral lamina of any specimen, just the two primary ones.

Prebranchial length contained 7-8 times in total length, branchial 9-10 times. Trunk length approximately half the total (contained 1.9 to 2.5 times in total). Tail length 3.0 to 3.7 times in total. Preorbital 1.5 to 1.7 in prebranchial. Eye diameter contained 5-8 times in prebranchial length, postorbital 3.4 to 4.5 times, oral 1.9 to 2.5 times.

The intestine of all specimens was empty and non-functional; gonads were mature or recently evacuated.

VARIATION: Table 1 shows the minima, mean and maxima of the body proportion characters of this species, in order to show the variation encountered and differences between this species and T. spadiceus. All specimens examined have two primary cusps on the supraoral lamina. One to six of typical circumorals frequently lacking. Variation of infraoral cusps (first figure refers to larger cusps, the second to smaller cusps, and figure in brackets to frequency): 5 + 0(3), 5 + 1(1), 5 + 2(6), 5 + 3(6), 5 + 4(7). Myotomes: 60(1), 61(1), 62(6), 63(3), 64(4), 65(2).

TYPE LOCALITY: Celio River, at Jacona, Michoacán, Mexico.

NAME: We propose the name T. geminis, meaning twins, to show that the new species greatly resembles T. spadiceus. Such paired species are characteristic of this class of animals.

DISCUSSION: A comparison of the morphological characters commonly used to identify Petromyzonidae species revealed at least five with statistical differences in the proportional values calculated for T. geminis and

T. spadiceus. The value found for "P" when calculating the difference in the mean was less than 0.05. Furthermore, as mentioned earlier, the allometric coefficient "k" was used to determine whether the character differences might be attributable to allometric growth. It was found that isogonic growth was applicable to branchial, preorbital and oral lengths, since the values for "k" approach unity, as shown in Table 1, and morphological differences between *T. spadiceus* and *T. geminis* do not derive from the different lengths of the species.

No specimen of the new species is longer than the longest larvae, i.e., 124
total length does not exceed 15 cm, while adults of *T. spadiceus* are always at least as long as the largest larvae.

Feeding habits also differ. Once metamorphosis begins, *T. geminis* eats nothing, spawning and dying three or four months after transformation. *T. spadiceus*, on the other hand, begins to feed on blood as soon as metamorphosis is complete, and continues to do so for two more years until the sexually-mature animal migrates to spawning grounds, mates and dies.

In our description earlier we noted the greater variation in dentition in *T. geminis*. The number of myotomes is also similar in both species: maximum frequency was 63, and specimens with 62 to 64 accounted for 75% of all individuals examined.

CUADRO 1. VARIACION Y COMPARACION DE *TETRAPLEURODON SPADICEUS* Y *T. GEMINIS*
TABLE 1. VARIATION AND COMPARISON OF TETRAPLEURODON SPADICEUS AND T. GEMINIS

	T. spadiceus					*T. geminis*					Indices		
	N	Mín.	Media MEAN	Máx.	Desv. Estánd. STANDARD DEVIATION	N	Mín.	Media MEAN	Máx.	Desv. Estánd. ST.DEV.	T	P	K
En milésimos de la longitud total / in thousandths of total length													
Prebranquial / Prebranchial	51	109	129.76	157	9.36	21	120	131.92	142	6.06	0.975	0.5	
Branquial / Branchial	53	82	100.86	136	9.61	22	93	107.73	116	6.19	3.1	0.01	1.00
Somática / Trunk	50	410	462.60	503	22.90	21	403	453.59	507	23.40	1.53	0.1	
Caudal / Tail	53	272	298.50	343	17.90	21	267	299.28	329	16.80	0.212		
En milésimos de la distancia prebranquial / in thousandths of prebranchial length													
Preorbital	32	575	659.36	700	10.93	9	578	630.00	678	18.90	6.16	0.01	1.20
Ocular	54	119	151.56	189	16.30	20	124	170.50	206	16.70	3.68	0.01	0.78
Postorbital	53	194	238.03	202	22.00	20	227	257.00	201	16.40	5.45	0.01	0.66
Oral	43	447	518.73	576	34.00	20	399	463.25	522	36.00	3.08	0.01	1.04

DESCRIPTION OF LARVAE

As no description of Tetrapleurodon ammocoetes has been published to date, we will now report the findings of an examination of 30 specimens gathered in Jacona, Mich. on January 13, 1963. Total length varied from 120 to 173 mm. These were the largest larvae available, and were probably 125
entering their third year. Since T. spadiceus and T. geminis larvae are indistinguishable, the following will apply to ammocoetes of both species.

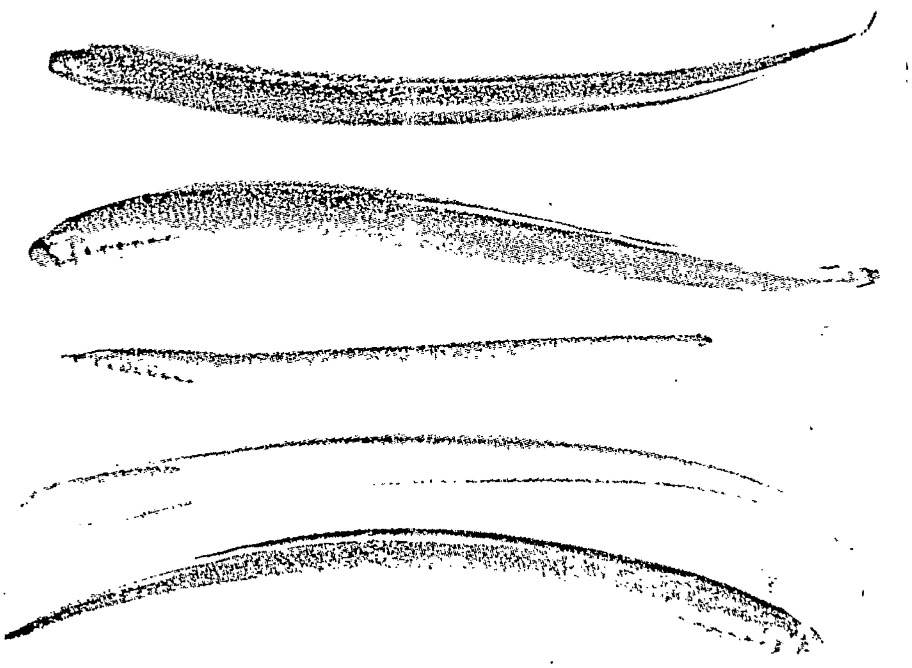


FIG. 6 Tetrapleurodon larvae showing no external signs of metamorphosis, captured in January 1963.

Table 2 shows the body proportions that can be identified in these organisms, used in every attempt to define and distinguish ammocoetes, and the variations recorded.

TABLE 2. CHARACTER VARIATION IN 30 TETRAPLEURODON AMMOCOETES HAVING A TOTAL LENGTH OF FROM 120 TO 173 mm

	IN THOUSANDTHS OF TOTAL LENGTH Min.	Mean	Max.	Standard Deviation
Prebranchial length	67	74.67	93	4.78
Branchial length	112	123.33	139	5.65
Trunk length	470	505.00	525	13.70
Tail length	272	287.33	312	13.20

Myotomes 61 (8), 62 (7), 63 (7), 64 (5), 65 (3).

COLORATION: The body is covered more or less uniformly by dark grey pigmentation extending over the upper lip, except for the dorsal fins, the full length of the ventral surface, including the caudal peduncle, and the subbranchial region, which are cream-coloured.

The unpigmented postnasal spot is rarely detectable, and is much smaller than the nostril. The prebranchial pigment patch is quite noticeable. Dorsal pigmentation of the cephalic region does not reach the gill openings. On lanceolate tail fin, pigment extends to outer edge of dermic rays, stopping short of fin edge, and with greater intensity along each ray; tail fin thus has a very narrow, light-coloured border. Some dark spots at base of second dorsal fin. No pigment found in the structure which Vladykov (1950) calls the tongue precursor.

LARVAL DEVELOPMENT

The breeding season begins in the month of November, when the water temperature is about 20°, and continues until the following January.

This affirmation is based on the fact that the gonads of adult specimens captured in the Duero River in October were fully mature and the intestine completely collapsed and showing clear signs of degeneration (Fig. 7). Additionally, a search at the uppermost reaches of the Celio River in Jacona, Mich. yielded very mature T. spadiceus adults migrating to the spawning grounds and other equally mature T. geminis; female ovaries in the latter case were packed with eggs or completely empty, a clear sign that spawning and fertilization were completed. Many of the T. geminis specimens were dead or dying, and the remains of many lampreys which had died a few hours or a few days earlier were found at the same site.

Samples of river mud brought to the laboratory in the latter half of November were found to contain minute eggs which appear to be from Tetrapleurodon, judging by their size and appearance.

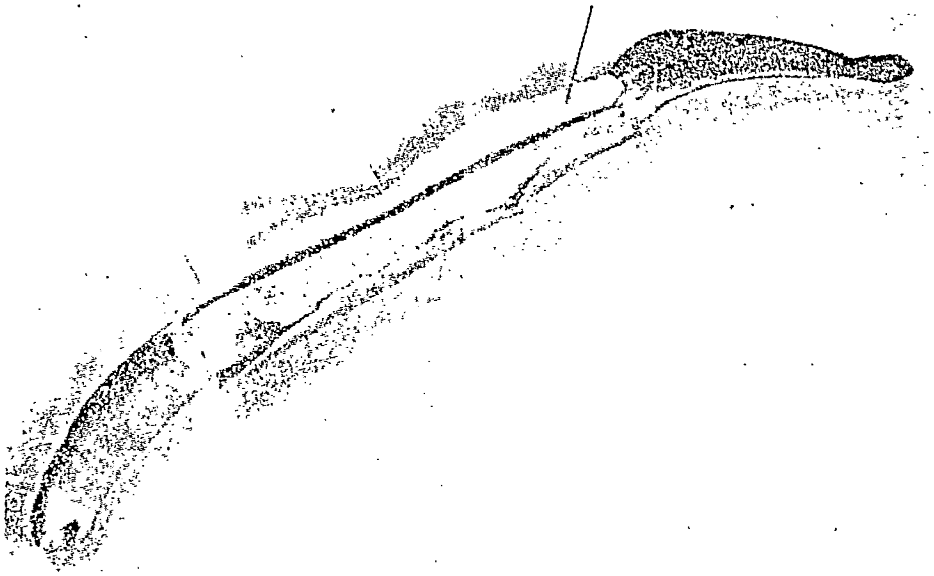


FIG. 7 Female adult T. spadiceus, dissected to show ovules filling abdominal cavity.

The smaller larvae, captured on November 18, are 9 mm long and approximately three weeks old, since according to Gage (1927: 413) lamprey eggs begin to develop several hours after fertilization, and depending on the temperature, the young hatch several days later. They remain in the nest until all or most of the vitelline reserve has been absorbed. Meanwhile, the heart, blood vessels, mouth, gills and digestive tract develop, and the larvae are then ready to feed on aquatic micro-organisms. After about three weeks, they are as slender as a pin and about 1 cm long.

A large number of specimens were captured on November 10, 1963 at the same spot at which mature adults, eggs in the stream bed and the smallest larvae had been found the same month in 1962. Only one and two-year old

larvae were detected in this material. While this would appear to contradict the affirmation in the previous paragraph, it can be seen 127
as an indication that the onset of the reproductive season may vary from year to year, although it will always be in the late fall, unlike other species in this family which have been seen to reproduce in early spring.

The end of the spawning season has been set in late January, since captures in early January still revealed mature T. geminis adults with empty gonads, and eggs were still detected in silt in the river bed. By the middle of that month, very few adults and no eggs at all were found.

Water temperature apparently does not determine the onset of reproductive activity. Although the only data available are temperature readings at the time of captures, temperature was relatively uniform and constant, ranging from 16.2 to 22.5 degrees; the lowest temperatures did not correspond to the coldest months or vice-versa. The very slight variation in temperatures recorded is probably explained by the fact that the capture site is located just over 1 km from the source of the river.

Eggs found in the mud are round, smooth and free of filamentous adhesions or any other external structure. Their diameter ranges from 0.8 to 0.95 mm, slightly larger than the 0.68-0.75 mm diameter of eggs extracted from mature females.

Tetrapleurodon mates and spawns in the headwaters of the Celio River, a choppy clear-water stream with a stony bed, forming small waterfalls alternating with rapids and generally small pools with substrates of plant detritus, silt and sand. The upstream limit of the breeding grounds appears to be a diversion dam that may prove insurmountable for animals in their spawning migration. While it is impossible to establish a downstream cut-off point, numerous searches have failed to reveal any eggs or larvae beyond the locality and area referred to above.

AMMOCOETE FEEDING APPARATUS AND HABITS: The anatomic structure of the anterior region of the digestive tract and a microscopic examination of the gut contents of many ammocoetes of different ages confirm that the larvae are plankton eaters.

A filtering apparatus at the anterior entrance to the alimentary tract, consisting of very branched fimbriae or cicumoral projections, serves as a screen which lets through only minute particles of silt and plankton, suspended in the water that is continually ingested by the ammocoetes.

This suspended matter then reaches the pharynx and its endostyle, which runs ventrally and longtitudinally in the pharyngeal cavity. The *Tetrapleurodon* endostyle is very well developed.

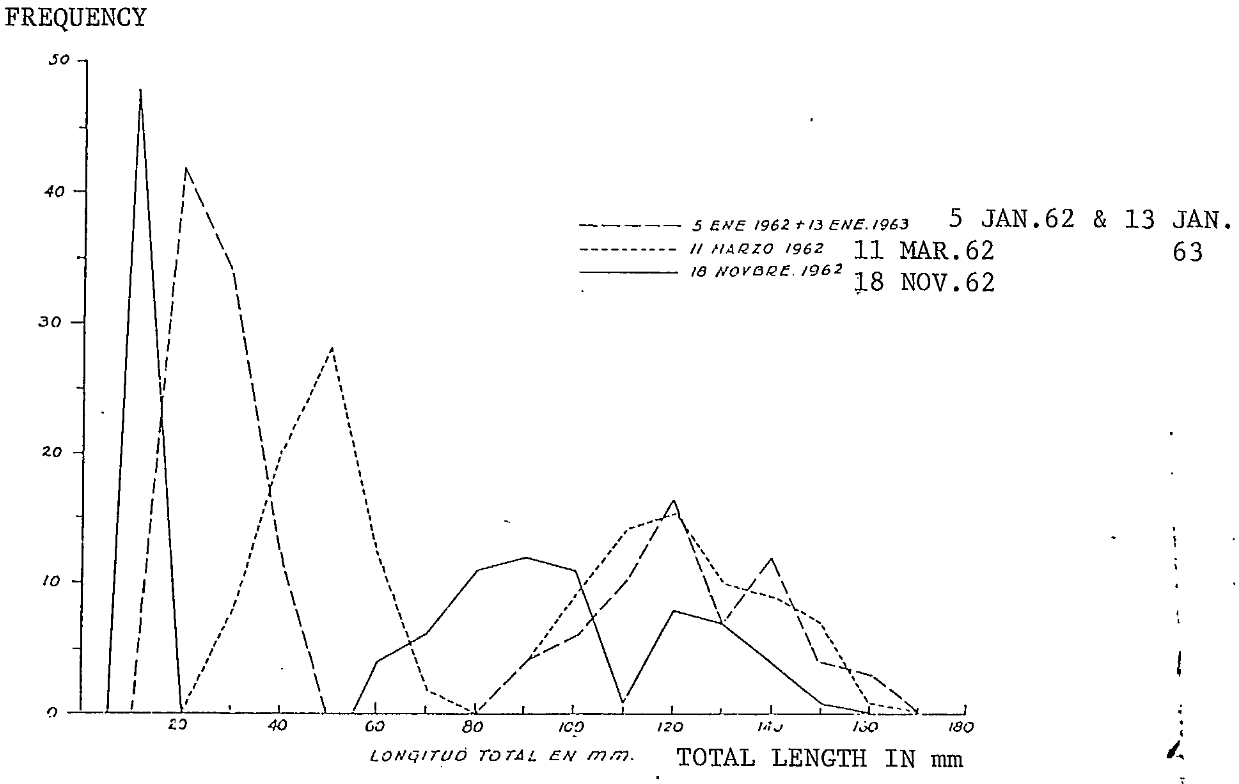
As stated previoysly, the larvae bury themselves in the river or stream bed. After burrowing into the mud head first, they trace a U-shaped curve and resurface with only the tip of the body protruding.

This behaviour, which has been documented by several authors in work 128
on other lamprey genera, was noted in the laboratory where five minute Jacona larvae were kept from January to March 1962. When a specimen was

stimulated, usually with a glass rod, it left the aquarium substrate, swam vigorously for a brief distance, and then buried itself again. With careful, patient observation, one could often see the anterior part of the ammocoete protruding from the aquarium liner material, very close by the original burrow hole. When the animal was disturbed slightly, its first reaction was always to shrink back into the surrounding substrate, but if that substrate itself was disturbed, the larva left the hole and buried itself once again.

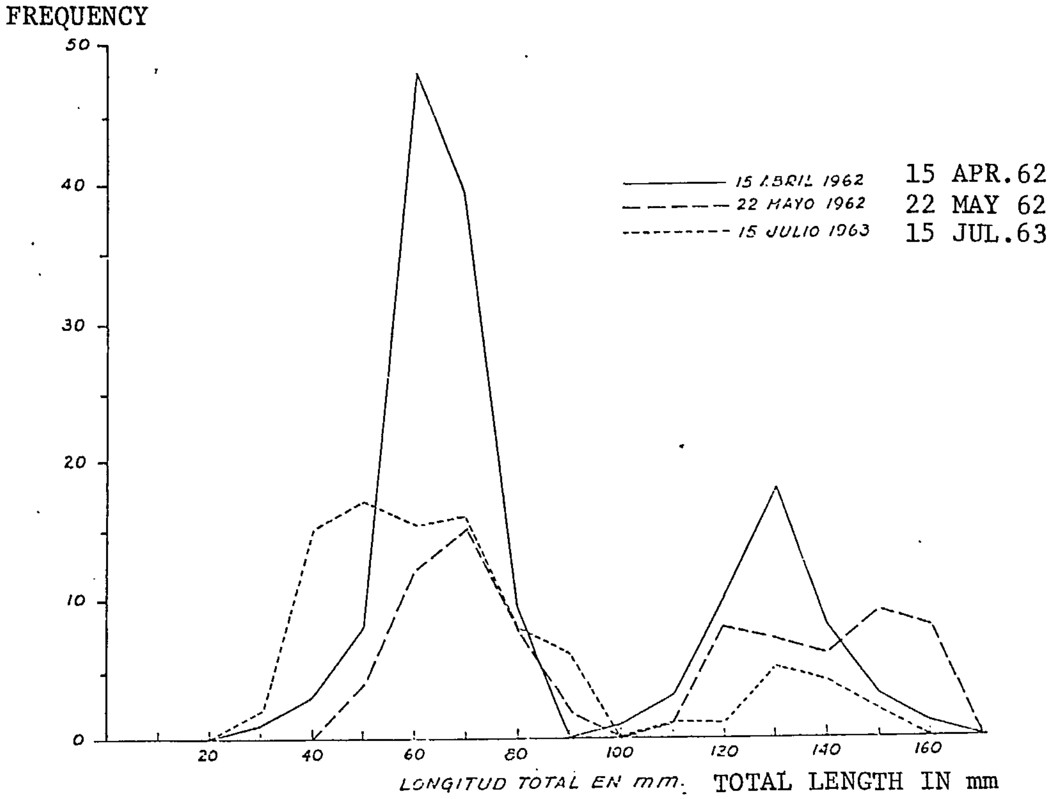
Small holes revealing the location of ammocoete burrows are easily spotted in the stream bed from which all of our larvae were taken; in fact, the existence of such holes was taken as an indication of the presence of specimens during capture expeditions. On a number of occasions the speed with which the larvae were seen to bury themselves in the mud or sand was quite astonishing.

An examination of the gut contents revealed large numbers of plankton, primarily algae of the genera Rhizosolenia, Pleurosigma, Pinularia, Stauroneis, Amphora and Cocconema, some pieces of filamentous chlorophyceae, rotifers, ciliates and the occasional euglenoid flagellate; no crustaceans or insect larvae were found, being no doubt too large to pass through the oral filter.



Graph 1. Length of Tetrapleurodon ammocoetes captured in Jacona, Mich., in November, January and March.

When the material extracted from the digestive tube was compared with material collected over the space of two hours from a plankton net set in the stream, the concentration of diatoms in the gut was found to be much higher than in the plankton sample.



Graph 2. Length of Tetrapleurodon ammocoetes captured in Jacona, Mich. in April, May and July.

Concentrations of such organisms in the intestine were also very different in larvae caught during the rainy season and those captured when water levels were low. Obviously, concentrations will be higher when there is less rain and less runoff.

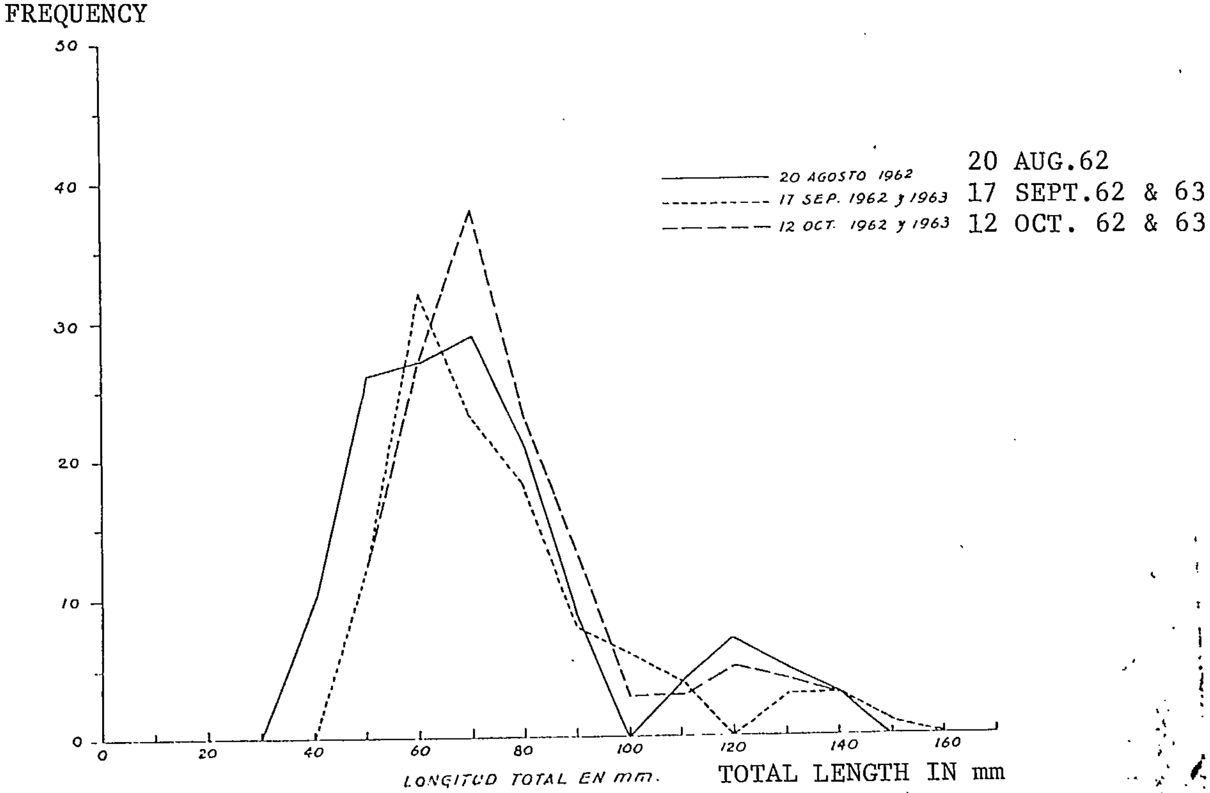
AMMOCOETE GROWTH: The dotted line in Graph 1 represents the size frequencies for larvae collected on November 18, 1962. Because the distribution is clearly trimodal and because November, as we have mentioned before, marks the onset of the breeding season, we have taken that month as the base month for an examination of growth.

The first mode of the distribution, including lengths of from 11 to 19 mm, clearly represents the youngest population; the second and third modes represent one and two-year-old individuals, respectively.

On the curves formed using the length values encountered in subsequent captures, the one-year class can be distinguished clearly, while the modes of the two older groups overlap. However, in some curves two modes can be distinguished in the upper ranges, and the destination of the three populations - so distinct in November - can still be traced, albeit with some difficulty.

A closer examination of the data shown in the graphs and taken from a study of the ammocoetes themselves will shed some light on this lack of clearly distinguishable modes.

First of all, the ammocoetes studied, like all animals, grow more quickly at the beginning of their life, and the growth rate slows with age. Since organisms slightly ahead of their year class in terms of growth will catch up to or overlap with those slightly behind in the next class, length frequency distributions tend to be unimodal or simple, even if two or more year classes are represented.



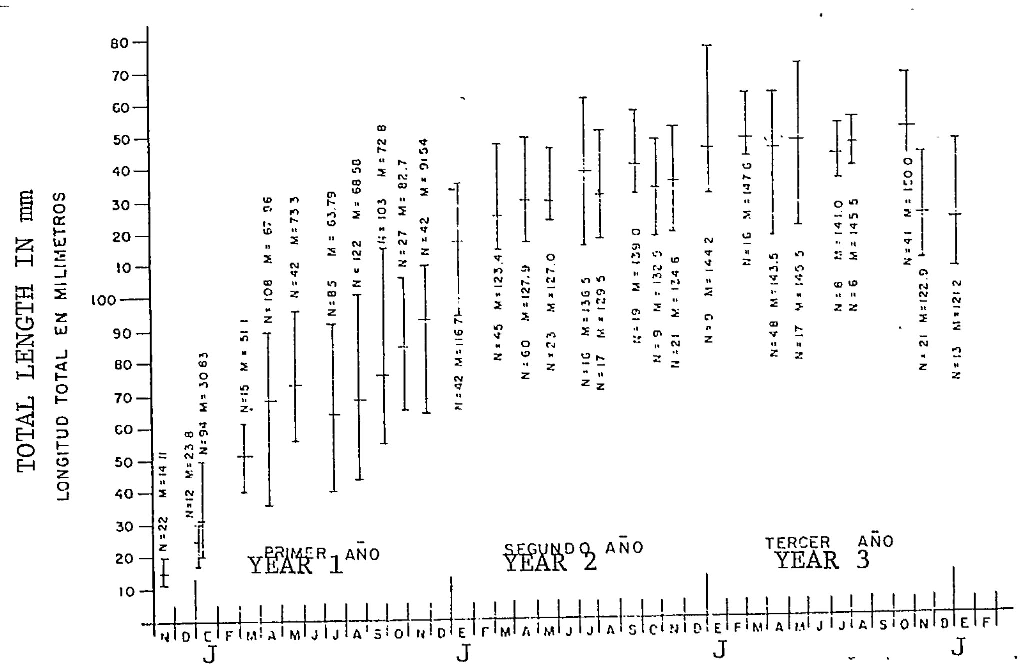
Graph 3. Length of Tetrapleurodon ammocoetes captured in Jacona, Mich. in August, September and October.

Three populations are clearly visible in the curve for January 131
(Graph 1) and even for March, but in April's representation (Graph 2), the distinct one-year group is accompanied by a second mode, the interpretation of which required an internal examination of the individuals.

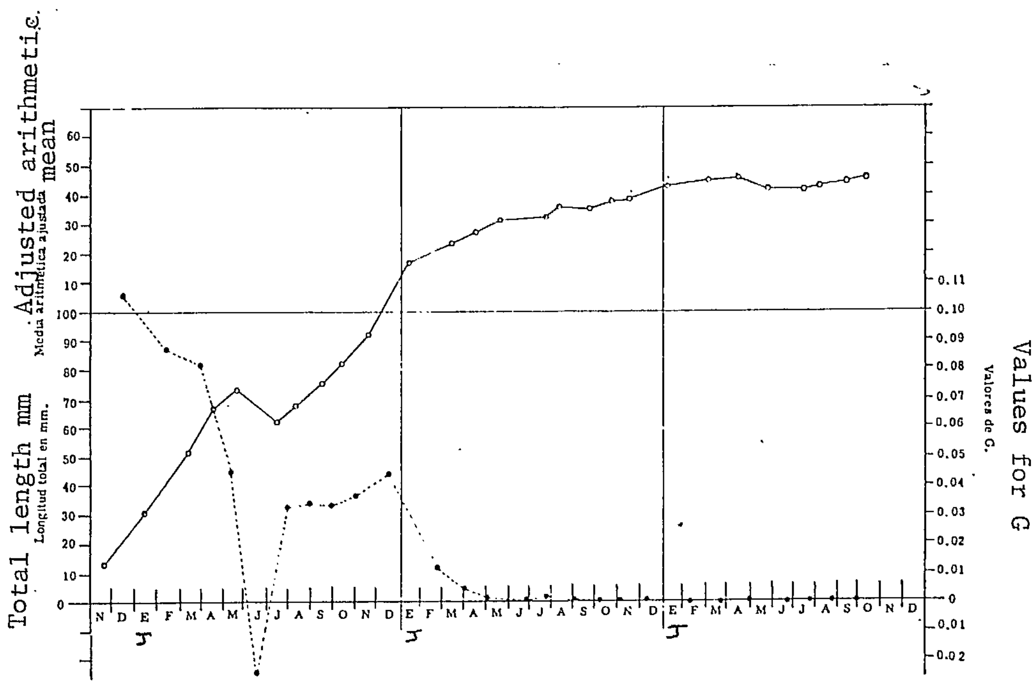
The dissection of ammocoetes captured that April revealed that the gonads were at an early stage of development and the digestive tract still full of food. According to Gage (1927), the process of sexual differentiation slows growth, making it difficult to distinguish between individuals of the second year class and those in their third year. This would explain the fact that the total length of larvae with visible gonads and that of sexually undifferentiated ammocoetes form statistically similar groups.

The same trend is evident in larvae captured in May, July and August (Graphs 2 and 3), but here we find more individuals undergoing metamorphosis, particularly in the July group. In some cases the process is almost complete, and in all instances the digestive tract is completely empty. According to some authors, this means not only that growth is inhibited but that total length diminishes, particularly in individuals of species which do not feed after metamorphosis; the transformation process is compounded in them by their rapidly maturing sexual organs.

Graph 4 shows length increase data over 34 months, from the smallest 132
ammocoetes captured in November to individuals obviously in the process of transformation, collected in August. The graph provides additional information on the length of mature and breeding T. geminis specimens, showing the decrease in length recorded towards the end of their life.



Graph 4. Growth of <u>Tetrapleurodon</u> ammocoetes over three years. The vertical lines show the range between observed minima and maxima; small cross-lines mark the arithmetic means calculated.



Graph 5. Growth distribution of <u>Tetrapleurodon</u> ammocoetes based on arithmetic means of year classes (solid line) and geometric growth rate (dotted line and solid black dots).

TABLE 3 - VALUES FOR GRAPH 5

CUADRO N° 3.—VALORES PARA LA GRAFICA N° 5

Etapa Stage	Edad dias Age-days	Lapso dias Days elapsed	N	Media mm Mean	Incremento mm Intervalo Interval (Increment)	Indice de crecimiento Growth rate Total	Aritm.	Geom.
I	?	0	22	14.11	—	—	—	—
II	60	60	106	30.13	16.02	16.02	0.28	0.109
III	117	57	15	51.31	21.18	37.20	0.37	0.089
IV	152	35	112	67.96	16.65	52.85	0.45	0.082
V	243	37	85	73.30	5.34	58.19	0.14	0.020
VI	264	54	122	63.79	−9.51	48.68	−0.09	−0.026
VII	317	21	103	68.58	4.79	53.47	0.19	0.034
VIII	336	19	27	72.80	4.22	57.69	0.41	0.011
IX	369	33	42	82.71	9.90	67.59	0.22	0.068
X	431	62	42	91.54	8.84	76.43	0.30	0.030
XI	488	57	45	116.70	25.16	101.59	0.14	0.039
XII	523	35	60	123.42	6.70	108.29	0.44	0.098
XIII	560	37	23	127.90	4.50	112.79	0.19	0.010
XIV	614	54	16	130.40	2.51	115.30	0.12	0.005
XV	635	21	17	130.70	−0.30	115.00	−0.04	−0.004
XVI	688	53	19	134.80	4.10	119.10	0.01	0.015
XVII	707	19	9	133.00	−1.80	117.30	−0.08	−0.0002
XVIII	740	33	21	135.00	2.30	119.60	0.03	0.0009
XIX	802	62	9	137.10	1.80	121.40	0.07	0.0004
XX	859	57	16	142.10	5.00	126.40	0.03	0.0005
XXI	894	35	48	145.10	3.00	129.40	0.08	0.0004
XXII	931	37	17	145.60	0.40	129.80	0.09	0.0001
XXIII	985	54	8	143.30	−2.20	127.60	−0.01	−0.0003
XXIV	1006	21	6	144.00	0.70	128.30	0.04	0.0009
XXV	1078	72	41	145.50	1.50	129.80	0.003	0.0004

The upper curve in Graph 5 consists of the adjusted arithmetic means taken from the data in Graph 4. Broadly speaking, the curve follows the standard pattern for this type of distribution: growth is noticeably rapid in the earliest stages of life, then slows and ultimately stops. This is 133
seen clearly in the lower curve of the graph, comprised of the values calculated for the daily geometric growth index during the period elapsed between each pair of consecutive captures, i.e. the percentage increase in mean total ammocoete length, if we consider that each increase attained immediately constitutes the base length on which the next following percentage increment will be calculated.

During the first years, except for negative values from May to July, the index varies from about 0.03 to just over 0.10, but from January on, when the ammocoetes are 12-14 months old, it slows considerably, and eventually disappears.

Halfway through the first year, larval length begins to shrink, from May until mid-July, when the geometric growth index dips below zero to almost -0.02. Once this critical stage has passed, the index again takes on positive values, comparable to those which it showed earlier.

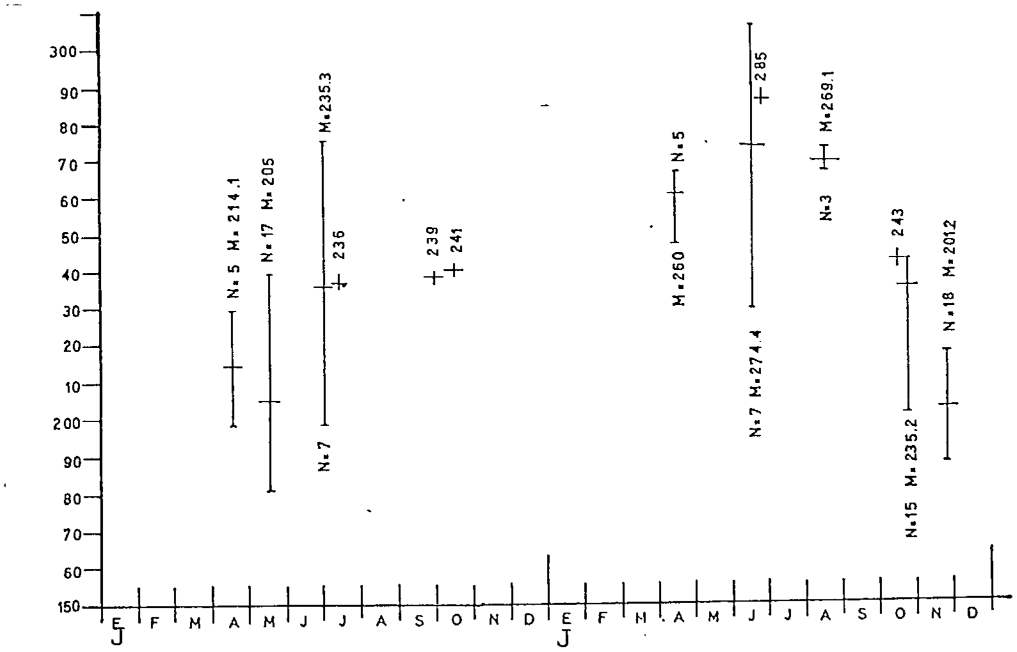
This typical decrease in length during the first year of life followed by an immediate return to positive ammocoete growth indices, here recorded for the first time in lampreys, is due probably to the influence of the rainy season on the ammocoete habitat. Abundant rainfall will not only raise the level of the Celio River substantially but will also mean more 134 silt suspended in its waters. On July 14, 1963, for example, the water level rose by just over two metres.

Large increases in water volumes have two additional effects: concentrations of plankton drop sharply, and the rushing water flushes away part or all of the concentrations of microorganisms normally found in still-water pools. Minute Tetrapleurodon thus must filter greater volumes of water to obtain the same amount of plankton available with much less effort when water levels are low and plankton concentrations higher.

Increased amounts of suspended inorganic material also mean less nutriment in the gut, even when full.

During our captures in the rainy season, particularly the July 15 expedition one day after the freshet mentioned above, we observed that the rushing water was carrying away portions of the sediment left by the torrent and that larvae which had been living there were swimming vigorously, usually against the current, in search of a suitable spot in which to bury themselves once again. This behaviour, which is repeated throughout the rainy season, naturally consumes vast amounts of energy.

In animals with a cartilaginous skeleton, such as the petromyzonts, food shortages of the type just described, coupled with fatigue, will translate into reduced length. The shorter lengths recorded do not appear to be accidental, since the same phenomenon was observed in specimens 135
captured the same month two years running, and the range of variation and arithmetic mean were very close.



Graph 6. Growth of T. spadiceus for two years after metamorphosis.

METAMORPHOSIS

April, May, July and August can be identified as the months in which metamorphosis takes place, based on examinations of specimens at different stages in the transformation process captured during those months.

The gonads of larger ammocoetes gathered in May show signs of differentiation, and this phenomenon is even more evident in the April specimens, so much so that it is sometimes possible to hazard a guess as to the individuals' sex without recourse to the microscope. Of 43 specimens dissected for this purpose, only twelve of the longest showed no signs of gonadal development. This can be interpreted in two ways: either T. spadiceus larvae are involved, or the specimens are very advanced members of the previous year class.

Some of the May specimens were obviously in the process of metamorphosis. The oral region lost the horseshoe shape typical of the larval stage and became circular; the fimbriae of the filtering apparatus disappeared, first on the dorsal side, then at the edges, and finally on the ventral border or labium. At an intermediate stage the filter apertures became noticeably larger than in the earlier stages. Cirrhi or lamellae appeared around the oral disk, and inside the disk the first dental structures began to appear, soft and fleshy until their keratin cover developed.

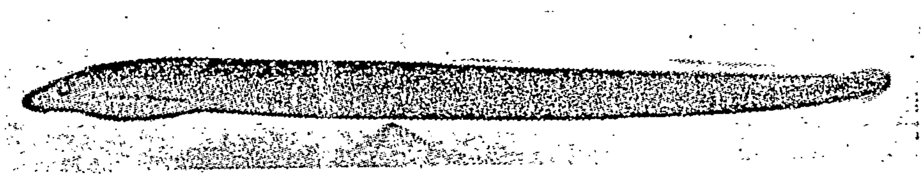


FIG. 8 Ammocoete obviously in the process of metamorphosis, captured in August. Eyes are clearly visible.

Internal changes are also visible. At the anterior end of the digestive tract the rasp develops from the "precursor", which is very weak in Tetrapleurodon species compared with Petromyzon marinus, Lampetra aepyptera and Entosphenus lamonttenii, of which Vladykov (1950, Fig. 13) published photographs. The common pharyngo-branchial conduits appear, as does a filter at the posterior end of the esophagus, so liquid ingested can reach the gill pouches bypassing the pharyngeal cavity, which loses its endostyle.

All of the specimens examined for this purpose and all those showing signs of metamorphosis had empty digestive tracts, although there was no evidence of degeneration.

The larva's eyes are lodged deep below the musculature; they become 136
apparent during metamorphosis, although they are still covered by the tegument.

In some specimens, probably of T. geminis, gonads were so well developed that eggs were perfectly discernible in females.

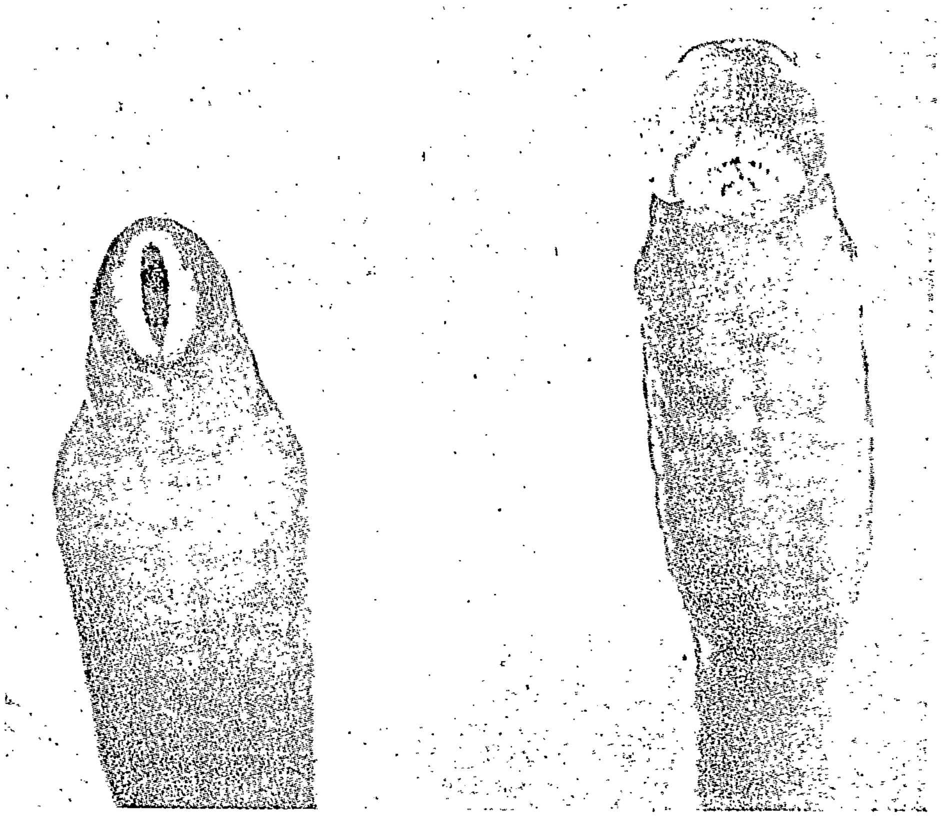


FIG. 9 Metamorphosis of buccal region. A - Near final stage of transformation, filter disappears, perioral tentacles appear, opening becomes circular. B - Untransformed larva: opening is horseshoe-shaped and filter is present.

FEEDING HABITS OF T. spadiceus: Thirty-five digestive tracts from lampreys over 200 mm long were examined. Twelve were found to be empty and collapsed because the individuals had reached sexual maturity. These were the longest individuals, collected in the Duero River near Zamora, in Jacona and in Chapala Lake, from October to November. Four had an empty gut but immature gonads: these individuals had likely completed the digestion process and had caught no new prey, since an examination of their organs failed to produce any evidence of degeneration. Two lampreys in which remains of digested blood were found in the intestine were probably in similar circumstances.

Seventeen guts examined were so filled with blood that the distended organ filled the entire abdominal cavity. In four of these individuals, the blood was mixed with a large number of scales, identified as having come in one case from the catostomid *Moxostoma austrinum* and in two others from a medium-sized cyprinid which was not *Cyprinus* or *Carrasius*, as these have a different type of scale. *Notropis* and *Algansea* were also eliminated as a source, since their scales are smaller. When the scales in the lamprey guts were compared with scales of the three remaining types of cyprinid recorded in Chapala and the Duero River, they appeared to resemble those of *Xystrosus popoche* more than *Falcularius chapalae* or *Yuriria alta*, to which they could also be attributed. Finally, the scales in the fourth lamprey were practically destroyed by the action of the gut, but we could hazard the guess that they were from an atherinid, a family represented in those watersheds only by the genus *Chirostoma*.

One digestive tract examined contained both eggs and cyprinid scales; bearing in mind that cyclostomes seek new prey only when they have fully digested their food, and that they feed until they are sated or have consumed all of the blood in their prey, we can state that eggs and scales came from a single individual.

The presence of scales and especially eggs   is a telling indicator of the severity of the wounds inflicted by lampreys on their temporary hosts in this extreme form of depradation.

MIGRATION AND GROWTH: The gonads of some ammocoetes which begin metamorphosis in April show no signs of development; these are probably *T. spadiceus* larvae.

The absence of adult or metamorphosing individuals either buried in the river bed or swimming freely at the upper reaches of the Celio River from September to November is an indication that as soon as these animals complete their transformation they migrate downstream towards the Duero, and the *marinus* type to Chapala Lake, where they remain for two years until sexual maturity.

The digestive tracts of five individuals ranging from 198 to 230 mm in total length, captured in April of 1962 in the Duero River, were found to be filled with blood and the gonads completely immature and practically undifferentiated. Although these animals are, on average, 50 mm longer than the larvae which underwent transformation the previous year, they are the smallest blood-eating adults we have; we assume that they are starting their fourth year of life.

Graph 6 shows growth data recorded for specimens from consecutive hauls. The stage of gonadal development and condition of the digestive tract were the factors used to distinguish the first blood-eating individuals, i.e. those entering their fourth year.

T. spadiceus is longest in late June and early July, probably two years 138
after metamorphosis. The longest individuals recorded by us measure 305 mm. These animals were captured in Chapala, presumably when they were about to migrate to spawning grounds; their gonads, which are at an early stage of development when migration begins, continue to mature en route. The *T. spadiceus* individuals taken from the Celio River in November were so mature that eggs spilled out when the animals were grasped.

MIGRATION OF *T. geminis*: It is interesting to note the absence of adults and individuals undergoing metamorphosis from September to early November at the capture sites referred to in this study and upstream towards a dam sitting near the source of the river and constituting an apparently insurmountable barrier for lampreys. We should mention that the water was clear and calm when our observations were made, so a careful search would have revealed any adults at the site, as did our expedition of November 18.

This absence of adults at the site at which metamorphosis took place and upstream from it during the period noted, compared with the large numbers of them observed at a later date, leads us to assume that they migrate with the current to the Duero River. After a period during which the gonads mature and the gut is compressed inside the abdominal cavity, the breeding lampreys migrate again to the source of the Celio River, where they spawn and die, at the same time and in the same place as individuals of *T. spadiceus*.

The migration process must be a very brief one, as it would be impossible for small lampreys to travel great lengths in a two-month span.

Support for this short-migration assumption is the capture on October 21, 1961 of four T. geminis individuals in the Duero River near its confluence with the Celio, only 3 km from the spawning grounds, all of the specimens being from 142 to 137 mm long and sexually mature.

This is the first time that migration of a planeri-type lamprey has been observed and verified. Researchers who have studied petromyzonts in other parts of the world (Gage, Cotronei, Okkelberg, Schultz, Vladykov, Zanandrea) report that adults of what they call the "non-parasitic form" transform ., mature, reproduce and die at the same sites.

FEEDING: The 31 T. geminis intestines examined were found to be shrunken, completely empty, and sometimes almost indiscernible amidst the large egg mass filling the abdominal cavity in females. This would appear to support the idea that the individuals who never feed on blood stop eating once they reach the height of metamorphosis in the month of July, and later 139
mate and die between November and January.

FECUNDITY: Abdominal cavities completely filled by gonads were found in five T. spadiceus females captured in Zamora, three on October 21, 1961 and two in November of 1962, and also in three T. geminis found in Jacona on November 19, 1962. These sexually mature animals were considered to be suitable specimens for relative fecundity calculations.

The counts and other data obtained are shown in Table 4.

DECREASE IN LENGTH: Mid-way through the last century, several researchers such as A. Meek, Rosmini and others recorded larvae longer than transformed specimens of the same species, a phenomenon which they attributed to individual variations. According to A. Meek (1916: 26) this shrinkage is necessary in metamorphosis. Some zoologists such as Lubosch, Van Beneden and Lomann (Cotronei 1927: 405) denied the existence of such a phenomenon, but numerous observations and the experimental work of Cotronei (op.cit. and 1926) have clearly confirmed that the length of petromyzonts diminishes during metamorphosis and sexual development.

Based on the data provided in Graphs 4 and 5, we can state that Tetrapleurodon is at its longest (176 mm) in January, when larvae are two years old or slightly older, and its length begins to shrink slightly thereafter, even though the mean value remains more or less constant in the samples examined.

Average growth trends persist until October, when the length begins to diminish considerably, particularly in specimens that are also nearing sexual maturity; adults of T. geminis captured in November and January measure only 106 to 145 mm, with an average of 121 mm.

We cannot at this time state exactly the length loss in millimetres of T. spadiceus during metamorphosis, but it would be reasonable to assume that it is comparable to or slightly less than that of T. geminis, since sexual maturity is not a factor in this case. The shrinkage during transformation is quickly made up, and the animal continues to grow for two years, as explained elsewhere in this article, until September, more or less, when it begins to mature and its length decreases by some 7 cm, if we are to judge by the measurements of July and August specimens (some 270 mm) and those individuals collected in spawning grounds in November (approximately 200 mm).

140

TABLE 4. FECUNDITY IN TETRAPLEURODON FEMALES

Ejemplar / Specimen		Ovario / Ovary			
Long. total mm / Total length mm	Peso en g / Weight g	Peso en g / Weight g	Ovulos por gramo / Eggs per g	Total óvulos / Total eggs	Indice / Index
T. spadiceus					
203	26.275	6.700	1 028	7 300	2.7
220	26.200	4.250	2 140	9 095	3.7
225	25.700	6.450	1 220	7 850	3.1
217	24.800	5.250	1 630	8 557	3.4
187	21.275	4.500	1 470	6 617	3.0
T. geminis					
148	7.000	1.600	2 160	3.456	4.9
133	4.300	0.450	2 200	990	2.3
108	5.100	2.100	1 424	2 200	4.3

A third length-loss stage, mentioned earlier in the section on larval growth, is the first year of life of the ammocoetes.

SEXUAL DIMORPHISM AND PROPORTIONS: The dorsal fins of sexually mature individuals are noticeably thickened and contiguous. The differences between sexes are perhaps clearest at this point: the females have a dermal fold like an anal fin, while in males a peniform sperm-conducting structure can be detected in the cloacal cavity and outside, although fertilization is strictly external. The oral disks of males are also slightly larger.

As has been observed in other genera (Schnackenberk 1929, Berg 1931, Vladykov 1949, Oliva 1953), these mature lampreys show signs of sexual dimorphism in the posterior region of the body, which curves down slightly in males but is straight or curved slightly upward in females, as illustrated in Figure 9, which shows two examples each of T. spadiceus and T. geminis.

We were able to determine the sex of 76 individuals (41 males and 35 females). The slight preponderance of males may be explained by the fact that during several expeditions specimens were taken from breeding grounds and even during courting, when males would naturally outnumber females.

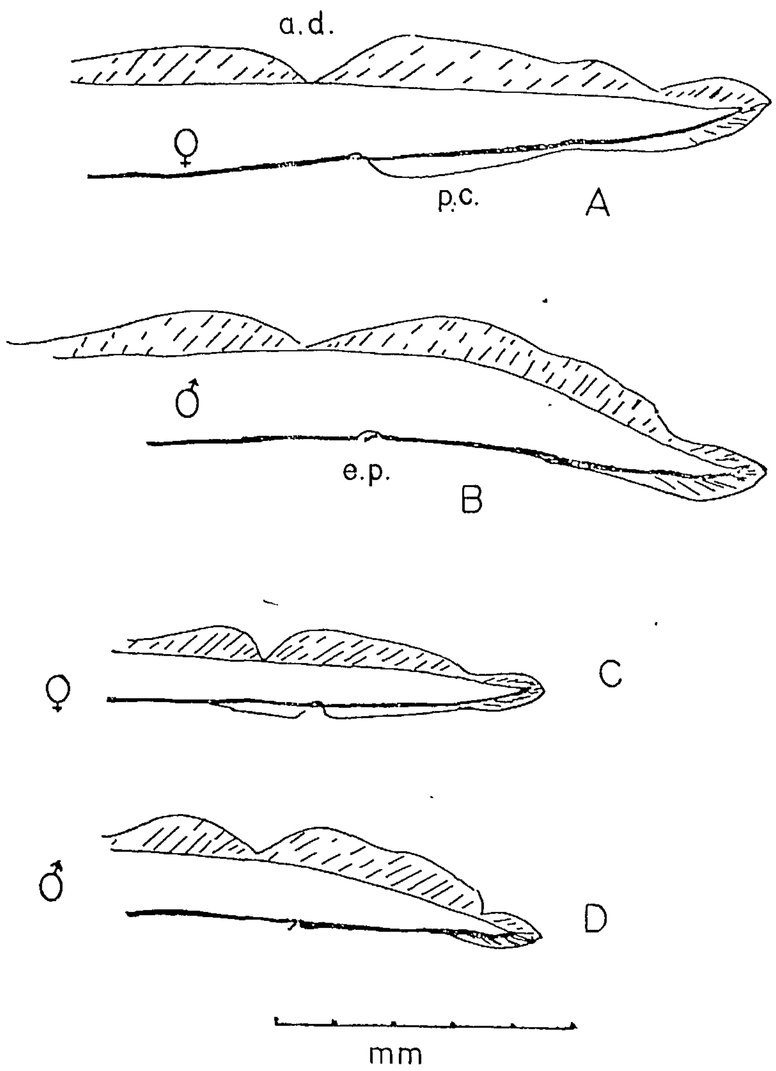


FIG. 10 Sexual dimorphism in Tetrapleurodon. A and B: T. spadiceus. C and D: T. geminis. a.d. - adjacent dorsal fins. e.p.- peniform structure. p.c. - caudal fold in females. Note curvature of tail region in males.

Summary

Based on one specimen sent from Guanajuato in western Mexico, by Dr. Dugès, T. H. Bean (1887) described a Petromyzonidae by the name of *Lampetra spadicea*. Dugès (1892) gave this lamprey the common name of "anguila de Jacona" thus pointing out the locality where it was captured by the writer.

For this study 1354 amocoetes larvae and nearly one hundred adults were captured at Jacona and Zamora, State of Michoacán, and at Lake Chapala, State of Jalisco, Mexico. A list of collection is included. Previusly only six specimens of *Lampetra spadicea* were known; three in the U. S. National Museum and three in the University of Guanajuato Museum.

Tetrapleurodon Creaser y Hubbs 1922, the genus to which these lampreys are assigned, has few anterior labial teeth which are arranged in concentric series. Generally two cusps are on the supraoral lamina. It differs from *Entosphenus* whose supraoral teeth are not arranged in concentric series. It has a strong intermedial cusp on the supraoral lamina, and the second and third circumoral de aticles are always tricuspid. *Tetrapleurodon* also differs from *Lampetra* in habing very few supralabial denticles, has only three circumoral denticles, the medial tricuspid and bicuspid the two other. The central cusp of the lingual lamina is notably larger in *Lampetra*.

DISTRIBUTION. Rio Duero in Michoacán and Jalisco, western Mexico.

Two species are in the genus; *T. spadiceus* (Bean) and *T. geminis* described here as new. The former is larger and of the "parasitic" type, whereas *T. geminis* is smaller, spawns after metamorphosis and dies. Variation of characters and comparison between the two species are included in table 1.

The description of the amocoetes larvae, common to both species, is given.

Tetrapleurodon spawns from November to January, at the head waters of Celio River, Jacona, Mich. The larval stage lasts three years. Growth of amocoetes is shown graphically. During the reiny season, the length of the amocoetes diminishes, especially those in their first year.

A short migration after metamorphosis of *T. geminis* is reported.

Data are presented on fecundity, food, growth, sexual dimorphism and other biological features for both species.

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