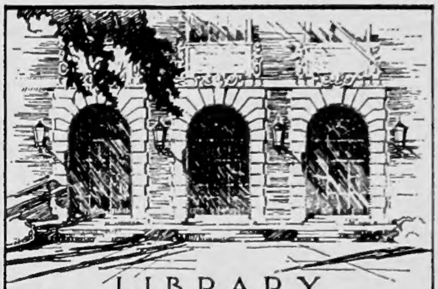


LIBRARY
OF THE
UNIVERSITY
OF ILLINOIS

NATURAL HISTORY
SURVEY

RELATIVE GROWTH IN POLYODON

David H. Thompson

STATE OF ILLINOIS
Department of Registration and Education
Division of the
NATURAL HISTORY SURVEY
Theodore H. Frison, Chief

BIOLOGICAL NOTES NO. 2 URBANA, JANUARY 1, 1934

Relative Growth in Polyodon

David H. Thompson

Rostrum.—The spoonbill cat, Polyodon spathula (Walbaum), has a broad, thin, paddle-shaped rostrum of cartilage enclosed in a loose network of bony splints. This great rostrum with its many sensory endings serves for the detection of plankton and other small organisms on which this fish feeds. The mouth is unusually large and the gill arches are furnished with numerous long gill rakers which strain out the food organisms as the fish swims about with its mouth open. It swims unceasingly with a monotonous rhythm and swings the rostrum from side to side in a wide arc. It has been supposed that these movements of the rostrum are of use in beating small animal life from vegetation in weedy lakes, but there is no evidence of any active digging.

Distribution.—Polyodon inhabits the Mississippi River, its connecting bottomland lakes and bayous, and the lower courses of its larger tributaries, including the Ohio, the Missouri, and the Illinois. It is a ganoid and resembles the sturgeons more than it does other native fishes. It has only one living near relative, Psephurus gladius, a large fish found in the Yangtze River in China. A fossil form, Crossopholis magnicaudatus, has been described by Cope (1883, 1885, 1886) from the Eocene Green River shales in Wyoming. Fossils of two specimens about a meter in length show snouts shorter than those of the two living forms (Dean, 1895).

Measurements.—In May, 1932 we collected seven larval specimens of Polyodon (Thompson, 1933) from which the length of rostrum and of body were measured. Extensive series of such measurements are given by Stockard (1907) and Danforth (1911). Barbour (1911) figured three specimens which have been measured, and Doctor N. Borodin has kindly furnished me measurements of three very small specimens in the Museum of Comparative Zoology at Harvard. Nichols (1916) published the measurements of a very large individual. These have been supplemented by measurements of other specimens in the collections of the Illinois Natural History Survey. Since these data form an unusually complete series, they show in some detail the relation between the length of rostrum and the length of body. This comparison of relative growth is of especial interest, since the rostrum is relatively very small in larvae, relatively greatest in specimens about 250 millimeters long, and becomes relatively shorter in larger individuals. The data are especially significant since the range of sizes is very great, the largest specimen being 127 times as long as the smallest specimen. Throughout all these sizes the spoonbill is free living, has no abrupt metamorphosis, inhabits the same waters, and feeds on the same food.

The following tabulation shows these measurements arranged in order of increasing total lengths. The rostrum and body

Relative Growth in Polyodon

David H. Thompson

Rostrum.—The spoonbill cat, Polyodon spathula (Walbaum), has a broad, thin, paddle-shaped rostrum of cartilage enclosed in a loose network of bony splints. This great rostrum with its many sensory endings serves for the detection of plankton and other small organisms on which this fish feeds. The mouth is unusually large and the gill arches are furnished with numerous long gill rakers which strain out the food organisms as the fish swims about with its mouth open. It swims unceasingly with a monotonous rhythm and swings the rostrum from side to side in a wide arc. It has been supposed that these movements of the rostrum are of use in beating small animal life from vegetation in weedy lakes, but there is no evidence of any active digging.

Distribution.—Polyodon inhabits the Mississippi River, its connecting bottomland lakes and bayous, and the lower courses of its larger tributaries, including the Ohio, the Missouri, and the Illinois. It is a ganoid and resembles the sturgeon more than it does other native fishes. It has only one living near relative, Psephurus gladius, a large fish found in the Yangtze River in China. A fossil form, Crossopholis magnicaudatus, has been described by Cope (1883, 1885, 1886) from the Eocene Green River shales in Wyoming. Fossils of two specimens about a meter in length show snouts shorter than those of the two living forms (Dean, 1895).

Measurements.—In May, 1932 we collected seven larval specimens of Polyodon (Thompson, 1933) from which the length of rostrum and of body were measured. Extensive series of such measurements are given by Stockard (1907) and Danforth (1911). Barbour (1911) figured three specimens which have been measured, and Doctor N. Borodin has kindly furnished me measurements of three very small specimens in the Museum of Comparative Zoology at Harvard. Nichols (1916) published the measurements of a very large individual. These have been supplemented by measurements of other specimens in the collections of the Illinois Natural History Survey. Since these data form an unusually complete series, they show in some detail the relation between the length of rostrum and the length of body. This comparison of relative growth is of especial interest, since the rostrum is relatively very small in larvae, relatively greatest in specimens about 250 millimeters long, and becomes relatively shorter in larger individuals. The data are especially significant since the range of sizes is very great; the largest specimen being 167 times as long as the smallest specimen. Throughout all these sizes the spoonbill is free living, has no abrupt metamorphosis, inhabits the same waters, and feeds on the same food.

The following tabulation shows these measurements arranged in order of increasing total lengths. The rostrum and body

Polyodon Measurements

Sources	Total length	Length of rostrum to front of eye	Length of body from front of eye	Rostrum as per cent of body length
	mm.	mm.	mm.	
Ill. Nat. Hist. Surv.	17.0	1.5	15.5	9.7
" " " "	17.5	1.2	16.3	7.4
" " " "	18.5	1.5	17	8.8
" " " "	19	1.6	17.4	9.2
" " " "	19	1.7	17.3	9.8
" " " "	20	1.7	18.3	9.3
" " " "	20	1.8	18.2	9.9
Borodin	37	8	29	27.6
"	57	15	42	35.7
"	60	19	41	46.3
Danforth	74	22	52	42.3
Barbour	80	24	56	42.9
Danforth	89	26	63	41.3
"	104	34	70	48.6
"	107	34	73	46.6
Barbour	130	46	84	54.8
Danforth	140	48	92	52.2
"	144	49	95	51.6
"	170	58	112	51.8
"	175	58	117	49.6
"	200	78	122	63.9
Ill. Nat. Hist. Surv.	200	69	131	52.7
" " " "	212	71	141	50.4
" " " "	215	69	146	47.3
" " " "	220	71	149	47.7
" " " "	225	78	147	53.1
" " " "	226	80	146	54.8
" " " "	227	82	145	56.6
" " " "	229	75	154	48.7
" " " "	230	79	151	52.3
" " " "	233	78	155	50.3
" " " "	233	83	150	55.3
" " " "	235	82	153	53.6
" " " "	240	89	151	58.9
" " " "	241	77	164	47.0
" " " "	248	83	165	50.3
" " " "	250	92	158	58.2
" " " "	252	88	164	53.7
" " " "	255	87	168	51.8
" " " "	261	89	172	51.7
" " " "	263	92	171	53.8
" " " "	266	85	181	47.0
" " " "	267	89	178	50.0
" " " "	270	92	178	51.7
" " " "	277	102	175	58.3
" " " "	309	113	196	57.7

Polyodon Measurements—continued

Sources	Total length	Length of rostrum to front of eye	Length of body from front of eye	Rostrum as per cent of body length
	mm.	mm.	mm.	
Ill. Nat. Hist. Surv.	410	131	279	47.0
" " " "	453	155	298	52.0
" " " "	514	152	362	42.0
" " " "	515	173	342	50.6
" " " "	526	177	349	50.7
" " " "	528	177	351	50.4
" " " "	531	180	351	51.3
" " " "	540	175	365	47.9
" " " "	543	160	383	41.8
" " " "	558	185	373	49.6
" " " "	577	188	389	48.3
Stockard	610	203	407	49.9
Ill. Nat. Hist. Surv.	621	199	422	47.2
" " " "	632	197	435	45.3
" " " "	752	236	516	45.7
Stockard	762	229	533	43.0
"	914	259	655	39.5
Barbour	914	245	669	36.6
Danforth	1,000	260	740	35.1
"	1,030	290	740	39.2
"	1,050	310	740	41.9
"	1,070	260	810	32.1
"	1,090	300	790	38.0
Stockard	1,118	305	813	37.5
Danforth	1,180	320	860	37.2
"	1,200	340	860	39.5
"	1,210	330	880	37.5
"	1,210	310	900	34.4
Stockard	1,245	333	912	36.5
"	1,295	343	952	36.0
Danforth	1,300	330	970	34.0
Stockard	1,346	343	1,003	34.2
"	1,499	356	1,143	31.1
"	1,524	404	1,120	36.1
"	1,575	406	1,169	34.7
"	1,600	400	1,200	33.3
"	1,600	419	1,181	35.5
"	1,676	400	1,276	31.3
"	1,702	432	1,270	34.0
"	1,753	454	1,299	34.9
Nichols	2,159	432	1,727	25.0

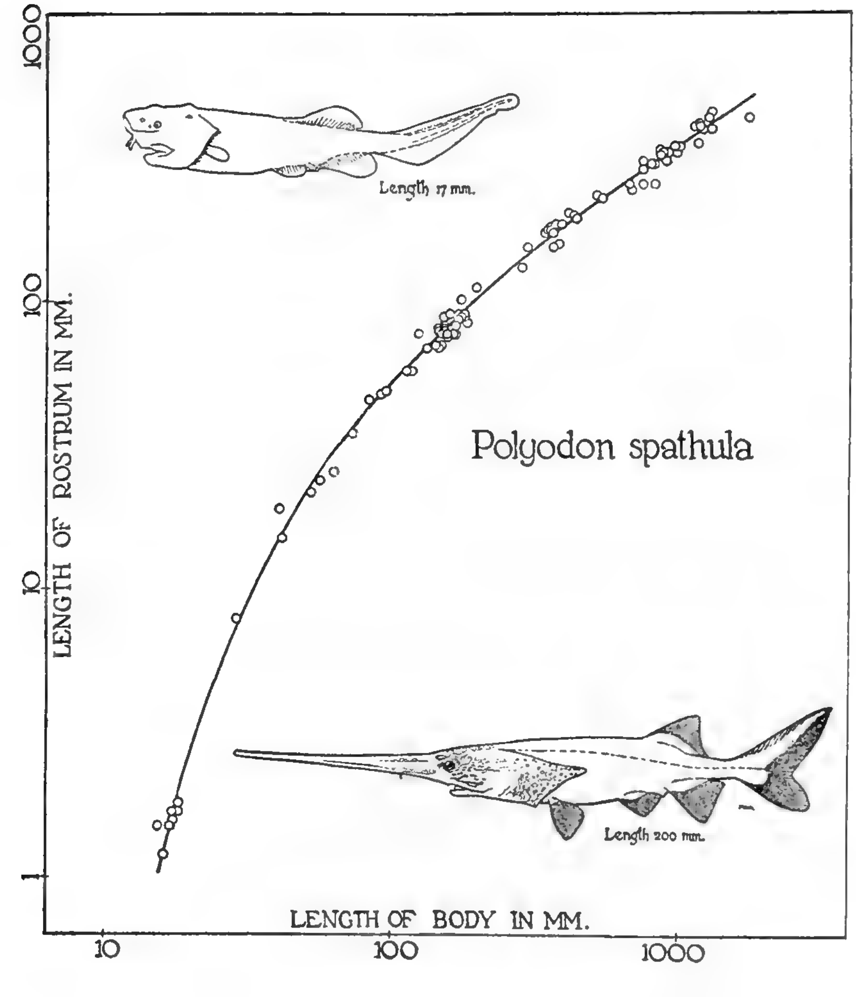
were measured from the front edge of the eye in order to be able to include published measurements. The eye is a well-defined base of reference for measurements in fishes and is particularly useful in growth studies since it is differentiated very early and is firmly anchored in the chondrocranium.

Differential growth.—In the accompanying figure, p. 5, the measurements of the length of rostrum are plotted against those of the length of body using the same logarithmic scale. An examination of the distribution of these points suggests a curve rather than a combination of two or three straight lines. Huxley (1932) has described a number of relative growth curves in which one straight line breaks abruptly into another straight line with a different slope. He also shows instances in which one straight line breaks into another through a short curve. May it not be that all such relative growth curves are hyperbolas with asymptotes crossing at varying angles and approaching these asymptotes more or less closely? It appears from inspection that the Polyodon measurements lie on an hyperbola whose asymptotes cross at an angle of about 135 degrees. A smoothed curve has been drawn by selecting the point where curvature is greatest and by drawing a symmetrical curve to the rather straight limbs at either end. The upper end of the curve, representing measurements of the larger specimens, is almost straight with a slope of 0.68. The lower end has a slope of about 4.1.

In order to learn something about the distribution of this differential growth within the rostrum of Polyodon, the length from the barbel to the eye was plotted against body length. This region was found to grow at the same rate as the body. Therefore, from the standpoint of relative growth, this part between the barbel and the eye will be considered as part of the body, since all of the heterogonic growth occurs in the part distal to the barbels.

The distance from the posterior edge of the eye to the tip of the opercular flap was measured on the specimens in the collections of the Illinois Natural History Survey and combined with other measurements made in the same way by Danforth (1911). When the logarithm of this length is plotted against the logarithm of body length one obtains a curve of heterogonic growth similar to that for the rostrum except that it shows smaller departures from isogonic growth. The slope of the lower limb of the operculum curve is about 1.9. It reaches a value of 1 at about the same body size as does the rostrum curve, and then declines slightly.

Barbel length was also measured throughout a wide range of sizes of spoonbill. When the logarithm of the length of barbel is plotted against the logarithm of length of body it may be seen that its relative rate of growth is at all times slower than that of the body within the size range of fishes used. The barbel curve begins with a slope of 0.7 but, in body lengths exceeding 100 millimeters, it has a slope of only 0.3. It should be mentioned that the barbel, like the rostrum and the opercular flap, is


Length 17 mm.
1000
100
10
1
LENGTH OF ROSTRUM IN MM.
Polyodon spathula
Length 200 mm.
LENGTH OF BODY IN MM.
10
100
1000

made up essentially of cartilage and skin. I should like to emphasize that the rostrum, the opercular flap, and the barbels each show declining rates of growth relative to the rest of the body.

Discussion.—Assuming an earlier stage in the development of Polyodon than has yet been discovered, a stage in which recognizable rudiments of the rostrum, opercular flaps, and barbels have not been differentiated, and keeping the relative growth curves of these organs in mind, an examination of the 17 millimeter specimen suggests that the barbels are differentiated first and go through an initial period of rapid development followed by declining growth rates relative to the rest of the body. Subsequently, the rostrum and opercular flaps are differentiated and grow at high initial rates which decline to the rate of the rest of the body or lower. Since barbels, opercula, and the rostrum each originate from cells, or groups of cells, with the capacity for synthesizing cartilage, it seems likely that the growth histories of these organs may be expressed as an equilibrium reaction between the total amount of growing cartilage in these organs and the concentration of cartilage-forming substances in the blood stream which feeds this cartilage.

Polyodon feeds on the same food throughout its life. Hence, it may be supposed that the digestive and assimilative processes remain the same throughout its life and, under comparable environmental conditions, that the amount of cartilage-forming substances put into the blood stream is closely proportional to the size of the body. Thus, we may expect that the actual concentration of these hypothetical cartilage-forming substances in the blood stream is greater in early stages of development, when there is little or no cartilage, than in later stages when there is relatively much cartilage to use them up by its mere subsistence. The rate of growth of these cartilaginous parts may then be expected to decline to the rate of the rest of the body.

While the assumption of an unutilized excess of cartilage-forming substances may account satisfactorily for the high initial growth rates of rostrum, barbels, and opercular flaps, and for the subsequent decline in the relative growth rate of these parts, it must be modified to account for the fact that the barbel curve has a slope of 0.3 in the same fishes which show rostrum and operculum slopes of approximately 1. In order to account for such differences in relative growth rates we may suppose that there are intrinsic differences in their component cells as regards their rate of multiplication, and since the barbels are attached to the rostrum, we may suppose that these intrinsic differences arise by some process akin to starvation. The same sort of explanation may be used to account for the decline in the rate of growth of the rostrum below that of the rest of the body. Polyodon shows an increasing proportion of rostrum until the fish has a total length of about 250 millimeters after which the proportion of rostrum declines. It has already been mentioned that the heterogonic

growth of the rostrum is limited to its distal part. One may look on this distal part as a growing tip—that there is isolated in the tip of the snout of a spoonbill larva a cell, or group of cells, which grow more rapidly than do those of the remainder of the animal; furthermore, that this cell, or group of cells, is carried forward by its own growth leaving behind it cell descendants which grow at the same rate as the rest of the body, i.e., more slowly. Since this growing tip apparently has the capacity to produce cartilage at a greater rate than its cell descendants in the same concentrations of cartilage-forming stuffs, it will tend to build up a surplus which cannot be maintained at an isogonic growth level once this growing tip is destroyed or is changed in its growth potentialities. As the gross amount of the cell descendants of this growing tip increases relative to the rest of the body, the blood supply reaching the tip must traverse more and more cartilaginous tissue and hence may become poorer and poorer in cartilage-forming substances. It seems reasonable that this starvation will reach a point where the growing tip is either destroyed altogether or is so altered that its cells no longer multiply more rapidly than those of other parts of the rostrum.

As one inspects the outstanding anatomical features of *Polyodon* in the material which we have available, it is apparent that the rostrum and the opercular flaps are the last organs to be differentiated. All other organs and major parts already have made their appearance and have passed through the initial stages of their growth history. We should look upon the heterogonic growth of the rostrum and the operculum as the normal growth behavior of parts which have been delayed in their differentiation while other large organs of the body have already been differentiated and have come into growth equilibrium with each other.

The rostrum is in a variable and unregulated condition. It may be looked upon as an organ which has been recently evolved and not yet coordinated with the rest of the body, or else, while it may be quite old, it has not been subjected to rigorous selective action. As one compares a series of specimens of *Polyodon* of the same body length one finds that such anatomical features as body contour, length, width, and insertion of fins, size of eye, and expanse of mouth are very uniform and fixed in their proportions. In contrast with the fixity of these morphological features the length of rostrum varies widely. It is apparent, however, that individuals with short rostra show a compensating increase in width. The lengths of opercular flaps not only vary from fish to fish but are usually different on the right and left sides. The rostrum of the spoonbill, as compared with the snouts of other fishes, may be considered as an organ which has undergone great changes since the ancestors of *Polyodon* split off from other fishes, and is twice as large as that of the Eocene spoonbill, *Crossopholis*.

The sturgeons are the nearest living relatives of the Polyodontidae, and, since sturgeons have snouts about the same size as that portion of the Polyodon snout between the barbel and the eye (which we have already shown grows at the same rate as the rest of the body) we may look on the remainder of the Polyodon rostrum as something added to the essential organization of a sturgeon-like fish. Since this added part appears late in development and is recognizable only insofar as it grows faster than the rest of the body, it may be considered as a sort of benign tumor which has become partially fixed in its characteristics and is in some degree useful as a bearer of sense organs for the detection of food. Like a tumor it may be removed without seriously hampering the welfare of the individual since we have found a number of specimens with various fractions of the rostrum cut off and healed over, as far back as the barbels.

BIBLIOGRAPHY

Barbour, Thomas. 1911 The smallest Polyodon.
Biol. Bull. Vol. 21, pp. 207-208.

Cope, E. D. 1883 A new Chondrostean from the Eocene.
Amer. Nat. Vol. 17, pp. 1152-1153.

1885 Eocene paddle-fish and Gonorhynchidae.
Amer. Nat. Vol. 19, pp. 1090-1091.

1886 On two new forms of Polyodon and Gonorhynchid fishes, from the Eocene of the Rocky Mountains.
Mem. Nat. Acad. Sci. Vol. 3, pp. 161-165.

Danforth, C. H. 1911 A 74 mm. Polyodon.
Biol. Bull. Vol. 20, pp. 201-204.

Dean, Bashford. 1895 Fishes, living and fossil.
Columbia Univ. Biol. Series. III Macmillan and Co.

Huxley, J. S. 1932 Problems of relative growth.
Methuen & Co., Ltd., London.

Nichols, J. T. 1916 A large Polyodon from Iowa.
Copeia. No. 34, p. 35.

Stockard, C. R. 1907 Observations on the natural history of Polyodon spathula.
Amer. Nat. Vol. 41, pp. 753-766.

Thompson, David H. 1933 The finding of very young Polyodon.
Copeia No. 1, pp. 31-33.

The sturgeons are the nearest living relatives of the Polyodontidae, and, since sturgeons have snouts about the same size as that portion of the Polyodon snout between the barbel and the eye (which we have already seen grows at the same rate as the rest of the body) we may look on the remainder of the Polyodon rostrum as something added to the essential organization of a sturgeon-like fish. Since this added part appears late in development and is recognizable only insofar as it grows faster than the rest of the body, it may be considered as a sort of benign tumor which has become partially fixed in its characteristics and is in some degree useful as a bearer of sense organs or in detection of food. Like a tumor it may be removed without seriously impairing the welfare of the individual since we have found a number of specimens with various portions of the rostrum cut off and healed over, as far back as the barbels.

BIBLIOGRAPHY

Barbour, Thomas. [illegible] The smallest Polyodon. Biol. Bull. Vol. [illegible], pp. 207-208.

Cope, E. D. [illegible] A new Chondrostean from the Eocene. Amer. Nat., Vol. [illegible], p. [illegible].

[illegible] Eocene paddle-fish and Gonorhynchidae. Amer. Nat., Vol. [illegible], pp. [illegible]-1091.

1886. On two new forms of Polyodon and Gonorhynchid fishes, from the Eocene of the Rocky Mountains. Mem. Nat. Acad. Sci., Vol. [illegible], pp. [illegible].

Danforth, C. H. [illegible] A [illegible] mm. Polyodon. Biol. Bull. Vol. [illegible], pp. 201-204.

Dean, Bashford. [illegible] Fishes, living and fossil. Columbia Univ. Biol. Series, III. Macmillan & Co.

Huxley, J. S. [illegible] Problems of relative growth. Methuen & Co., Ltd., London.

Nichols, J. T. [illegible] A large Polyodon [illegible]. Copeia. No. [illegible], p. [illegible].

Stockard, C. R. [illegible] Observations on the natural history of Polyodon spathula. Amer. Nat. Vol. [illegible], pp. [illegible].

Thompson, David H. [illegible] The finding of very young Polyodon. Copeia No. 1, pp. [illegible].