The Development of Lepidosteus. Part I
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IV.

## THE DEVELOPMENT OF LEPIDOSTEUS.

By Alexander Agassiz.

Presented Oct. 8, 1878.

## PART I.

It has been my good fortune this spring to succeed in hatching Lepidosteus from the egg, and in raising. the young until they showed externally, at least, the principal structural features of the adult.

Like many other American naturalists, I had for many years been on the lookout for the breeding-places of our Lepidosteus and Amia; but although it was generally known that during the last part of May they appeared in large numbers in the Potomac, as well as in many Western rivers, and also in parts of the great lakes, no one had been fortunate enough to catch these fish while spawning. It was therefore with great expectations that I sent Mr. S. W. Garman to Ogdensburgh, N. Y., when Mr. S. S. Blodgett informed me that the garpike usually appeared on the 20th of May for the purpose of spawning. Mr. Blodgett did all in his power to make the expedition a success; and he has not only my thanks, but will have those of all naturalists, for the aid he has given so effectually in obtaining this ichthyological prize.

The following notes by Mr . Garman describe the method of spawning:-
"Black Lake is well stocked with bill fish. When they appear, they are said to come in countless numbers. This is only for a few days in the spring, in the spawning season, between the 15th of May and the 8 th of June. During the balance of the season, they are seldom seen. They remain in the deeper parts of the lake, away from the shore, and, probably, are more or less nocturnal in habits. Out of season, an occasional one is caught on a hook baited with a minnow. Commencing with the 20th of April, until the 14th of May we were unable to find the fish, or to find persons who had seen them during vol. xiv. (n. s. vi.)
this time. Then a fisherman reported having seen one rise to the surface. Later, others were seen. On the afternoon of the 18th, a few were found on the points, depositing the spawn. The temperature at the time was $68^{\circ}-69^{\circ}$ on the shoals, while out in the lake the mercury stood at $62^{\circ}-63^{\circ}$. The 'points' on which the eggs were laid were of naked granite, which had been broken by the frost and heat into angular blocks of three to eight inches in diameter. The blocks were tumbled upon each other like loose heaps of brickbats, and upon and between them the eggs were dropped. The points are the extremities of small capes that make out into the lake. The eggs were laid in water varying in depth from two to fourteen inches. At the time of approaching the shoals, the fish might be seen to rise quite often to the surface to take air. This they did by thrusting the bill out of the water as far as the corners of the mouth, which was then opened widely and closed with a snap. After taking the air, they seemed more able to remain at the surface. Out in the lake they are very timid, but once buried upon the shoals they become quite reckless as to what is going on about them. A few moments after being driven off, one or more of the males would return as if scouting. If frightened, he would retire for some time; then another scout would appear. If all promised well, the females, with the attendant males, would come back. Each female was accompanied by from one to four males. Most often a male rested against each side, with their bills reaching up toward the back of her head. Closely crowded together, the little party would pass back and forth over the rocky bed they had selected, sometimes passing the same spot half a dozen times without dropping an egg, then suddenly would indulge in an orgasm ; and, lashing and plashing the water in all directions with their convulsive movements, would scatter at the same instant the eggs and the sperm. This ended, another season of moving slowly back and forth was observed, to be in turn followed by another of excitement. The eggs were excessively sticky. To whatever they happened to touch they stuck, and so tenaciously that it was next to impossible to release them without tearing away a portion of their envelopes. It is doubtful whether the eggs would hatch if removed. As far as could be seen at the time, upon or under the rocks to which the eggs were fastened, there was an utter absence of any thing that might serve as food for the young fishes.
"Other fishes, bull heads, \&c., are said to follow the bill fish to eat the spawn. It may be so. It was not verified. Certainly the points under observation were unmolested. During the afternoon of the

18th of May, a few eggs were scattered on several of the beds. On the 19 th , there were more. With the spear and the snare, several dozens of both sexes of the fish were taken. Taking one out did not seem greatly to startle the others. They returned very soon. The males are much smaller than the average size of the females; and, judging from those taken, would seem to have as adults greater uniformity in size. The largest taken was a female, of four feet one inch and a half in length. Others of two feet six inches contained ripe ova. With the 19th of May, all disappeared, and for a time the weather meanwhile being cold and stormy - there were no signs of their continued existence to be met with. Nearly two weeks later, on the 31st of May, as stated by Mr. Henry J. Perry, they again came up, not in small detachments on scattered points as before, but in multitudes, on every shoal at all according with their ideas of spawning-beds. They remained but two days. During the summer it happens now and then that one is seen to come up for his mouthful of air; beyond this there will be nothing to suggest the ravenous masses hidden by the darkness of the waters."

To Mr. Garman I am greatly indebted for the care with which he transported a quantity of garpike eggs contained in two pails which had to be carried by hand from Ogdensburgh to Cambridge, and for the arrangements made with Mr. Perry for collecting a series of eggs and of young fishes in all stages from the time of spawning until the end of July.

The present paper is, of course, merely a preliminary account, and I hope to give on another occasion a full description of the early stages of the egg, as well as a more detailed description of the changes the young undergo. Of the eggs brought to Cambridge, only thirty hatched. In my anxiety lest this attempt should fail, I did not dare to examine any of the fresh eggs; and from an external examination little or nothing of the early stages of segmentation and of the development could be traced on account of the opacity of the envelope of the egg. Not one of the eggs artificially fecundated was hatched, and only a few of those laid on the angular blocks (mentioned by Mr. Garman) lived to complete their development. The eggs were all attacked by mould, and decomposed rapidly in spite of the most watchful care. The few which did hatch, however, fully rewarded my efforts and fulfilled my anticipations. The young fish were quite hardy and flourished admirably. Of the thirty hatched in the latter part of May, no less than twenty-eight lived till the middle of July. They were exceedingly hardy, and, had it been possible to
feed them on minute fresh-water Entomostraca, I have no doubt they would have continued in excellent condition. During the whole time of the resorption of the yolk-bag, not a single individual was lost. It was only subsequently, when they had been fed for a while on liver, that they showed symptoms of poor condition; and finally they refused to eat it and languished for a few days, although at first they had eaten it apparently with great relish.

The eggs were laid on the 20th of May; when they reached Cambridge, they were still semi-transparent, the yellowish-green sticky outer envelope measuring about $5^{\mathrm{mm}}$ in diameter; the yolk-mass, of a whitish-blue color, was $3^{\mathrm{mm}}$. In their general appearance, the eggs resembled those of toads. They were attached to the stones just as they dropped from the females, in groups irregularly arranged or isolated.

On the 28th of May, the first young Lepidosteus was hatched (Plate I. fig. 1). The young fish possessed a gigantic yolk-bag, and the posterior part of the body presented nothing specially different from the general appearance of a Teleostean embryo, with the exception of the great size of the chorda. The anterior part, however, was most remarkable; and at first, on seeing the head of this young Lepidosteus, with its huge mouth cavity extending nearly to the gillopening, and surmounted by a hoof-shaped depression edged with a row of protuberances acting as suckers (Plate I. fig. 3), I could not help comparing this remarkable structure, so utterly unlike any thing in Fishes or Ganoids, to the Cyclostomes, with which it has a striking analogy. This organ is also used by Lepidosteus as a sucker, and the moment the young fish is hatched he attaches himself to the sides of the dish, and there remains hanging immovable ; so firmly attached, indeed, that it requires considerable commotion in the water to make him loose his hold. Aerating the water by pouring it from a height did not always produce sufficient disturbance to loosen the young fishes. The eye, in this stage, is rather less advanced than in corresponding stages in bony fishes ; the brain is also comparatively smaller, the otolith ellipsoidal, placed obliquely in the rear above the gill-opening. This is at first a mere small elliptical opening, which subsequently becomes heart-shaped (Plate I. fig. 11) with the development of the gill-arches, one of which is formed by the anterior part of the gill-opening, while two smaller ones are formed behind it (Plate I. fig. 6) much as in Sharks, except that we have a gill-cover in Lepidosteus as in bony fishes, which completely hides the gill-arches from view, when seen in profile. It is only when seen obliquely from
above that the gills can be seen behind the operculum, or when they are separated from the body in breathing (Plate II. fig. 16). Usually the gill-cover is pressed closely against the sides of the body, but in breathing an opening is seen (Plate IV. fig. 37) through which water is constantly passing, a strong current being made by the rapid motion of the pectorals, against the base of which the extremity of the gill-cover is closely pressed (Plate IV. fig. 42). The large yolk-bag is opaque, of a bluish-gray color. The body of the young Lepidosteus is quite colorless and transparent. The embryonic fin is narrow, the dorsal part commencing above the posterior end of the yolk-bag; the tail is slightly rounded, the anal opening nearer the extremity of the tail than the bag. The intestine is narrow, and the embryonic fin extending from the vent to the yolk-bag is quite narrow. In a somewhat more advanced stage (Plate I. fig. 3), - hatched a few hours earlier, - the upper edge of the yolk-bag is covered with black pigment cells, and minute black pigment cells appear on the surface of the alimentary canal. There are no traces of embryonic fin-rays either in this stage or the one preceding; the structure of the embryonic fin is as in bony fishes - previous to the appearance of these embryonic fin-rays - finely granular. Seen in profile, the yolk-bag is ovoid; as seen from above, it is flattened (Plate I. fig. 1), rectangular in front, with rounded corners, tapering to a rounded point towards the posterior extremity, with re-entering sides (Pl. I. fig. 7).

The head seen from above is rounded anteriorly, fringed by the row of suckers which form a connected, thickened margin; the eyes scarcely project beyond the general outline of the head; the gill-covers are small lobes immediately behind the eyes. The brain occupies but a comparatively small part of the head; the olfactory lobes are greatly developed, and elongated much as in Sharks and Skates, the posterior extremity of the brain rising obliquely towards the back and leaving a considerable distance between the base of the brain and the termination of the chorda, which ends between the otoliths (Plate I. figs. 6-11).

The second day after hatching, we can detect (Plate I. fig. 11) the first trace of an upward curve to the extremity of the tail. Up to this time, the chorda is straight, as is the embryo of any newly hatched bony fish; the yolk-bag has also greatly decreased in size; the head makes a less sharp angle with the longitudinal axis; the snout formed by the sucking-disk projects well beyond the outline of the opening of the mouth; the gill-opening is heart-shaped, and the heart can distinctly be seen to beat at the junction of the yolk-bag
with the lower part of the mouth cavity; the embryonic fin has broadened, and extends further along the back towards the head; the muscular bands surrounding the chorda are far better defined, and a few black pigment spots have also made their appearance at the base of the anal fin; the eye has become more distinct, and the nostrils are seen as elliptical pits close to the eye as in the earlier stage.

On the third day, the young Lepidosteus, when seen in profile, has a triangular yolk-bag (Plate II. fig. 13), greatly reduced in size from the previous stage; the whole body is covered with minute black pigment cells, more numerous towards the head and along the dorsal side; the gill-covers are now large rectangular flaps (see also Plate II. fig. 12), and we find in this stage the first trace of the pectorals. These appear at first at a distance from the body on the upper surface of the yolkbag (Plate II. fig. 12) as slight curlings of what we may call a lateral fold, indicated by a spiral line on the upper part of the yolk-bag. Seen in profile (Plate II. fig. 13), they stand up vertically, forming slight protuberances above the general surface of the yolk-bag. The eyes are more prominent; the whole snout has become more elongated than in previous stages; and the sucking-disk is more prominent than in younger stages, - the individual suckers projecting frequently far beyond the general outline of the edge of the sucker, when the young fish holds to any surface to which it may firmly have attached itself. The outline of the tail, or of the embryonic fins, has not altered from the preceding stage.

The young Garpikes would find it most inconvenient to move about with the huge yolk-bag with which they are provided; and although when disturbed they are powerful swimmers, propelling themselves much after the manner of tadpoles, by vigorous strokes of the tail, yet they remain until much later in life nearly constantly attached to the sides or bottom of the jars in which they are kept; and, if disturbed, will, after swimming round rapidly a few moments, hasten to attach themselves again to some suitable surface, where they remain hanging motionless during the greater part of the time till the yolk-bag has been completely resorbed. Their hold on the sides of the jar was so strong that they would remain suspended after the water had been lowered below the level to which they were attached.

Two days later, the yolk-bag has become still further reduced, especially under the gill-covers (Plate II. fig. 14) ; the trend of the head also makes a larger angle with the axis; the eyes have become more prominent; the gill-covers have greatly lengthened (Plate II. fig. 15),
and the pectorals have increased in size. The whole body is more thickly covered by black pigment cells: they are most numerous near the region of the head, along the dorsal line, and over the intestines and the upper part of the yolk-bag, making a strong contrast to its yellowish-gray color underneath. The curvature of the tail has increased, and four patches of pigment spots have appeared (Plate II. fig. 14). These are the first traces of the permanent fins, - the dorsal, the caudal, and anal, - the last spot on the dorsal side of the tail forming the spot of the temporary caudal lobe. The gill-arches in this stage (Plate II. fig. 16) are thin, short, club-shaped appendages, seen on certain portions behind the gill-covers.

The great development taken by the sucking-disk is best shown in a view from the lower side. The cavity of the mouth is seen (Plate II. fig. 17) to occupy the greater part of the lower side, between the sucker and the base of the yolk-bag, where the heart is placed. Five or six days afterwards, the cavity of the mouth has become reduced to a small (Plate II. fig. 18) trapezoidal opening; the gill-covers nearly meet on the lower side, near the median line; and in this stage the individual suckers of the sucking-disk are capable of great expansion, projecting, after the young fish has remained attached for a time, far beyond the general outline of the anterior part of the head. When seen in profile (Plate III. fig. 19), the outline of the head has assumed a most peculiar appearance, having certainly no resemblance whatever to the shape of the head in the adult. The yolk-bag has become much reduced in size; the pectorals have now assumed the characteristic Crossopterygian features; the eye is quite prominent; the lower jaw projects slightly beyond the former level of the mouth cavity; and there is also a short upper jaw, terminating in the huge swollen snout, covered with warts, forming the powerful sucking-disk. The gillcover is still more elongated than in previous stages, and there are short branches to the primary gill-arches. The whole body is now thickly covered with black pigment cells. These cells are, however, still most numerous above the eye, toward the dorsal region, along the upper part of the yolk-bag, where they are so closely packed as to form a dense black band, which is continued on the lower side of the chorda to the extremity of the tail. The black spots of the primary fins have expanded to form definitely shaped patches indicating the growth of the permanent fins, of which they are the rudiments. The extremity of the tail has a more marked heterocercal character, and both above and below the tail carries a large white patch completely surrounded by the darker pigment-cells. The fleshy lobe of the pec-
torals is bluish, as well as the outer edge of the gill-cover. We find also in this stage the first trace of the brilliant white pigment-spots which become the enamelled lines and spots so characteristic of somewhat older stages. In these young, they are found mainly on the sides of the gill-cover and along the line of the chorda on the anterior part of the body.

The next changes are mainly in the lengthening of the snout; the increase in length both of the lower and upper jaw (Plate III. fig. 23 ) ; the concentration of the suckers of the sucking-disk (Plate III. figs. 22, 24) ; and the adoption of the general coloring of somewhat older fish. The lobe of the pectoral has become specially prominent (Plate III. fig. 21), and the outline of the fins is now indicated by a fine milky granulation. Seen from above (Plate III. fig. 20), the gill-cover is seen to leave a large circular opening leading to the gillarches, into which a current of water is constantly passing, by the lateral expansion and contraction of the gill-cover; the outer extremity of the gill-cover covers the base of the pectorals (Plate III. fig. 26). In a somewhat older stage, the snout has become more elongated (Plate III. fig. 29), the suckers more concentrated, and the disproportionate size of the terminal sucking-disk is reduced; the head, when seen from above, becoming slightly elongated and pointed.

In the next stage, when the young Lepidosteus is a little over three weeks old (Plate III. fig. 30), the young has assumed a more fish-like form; the sucking snout is now reduced to a swelling of the extremity of the elongated upper jaw ; the lower jaw has also greatly lengthened; the fleshy part of the pectoral has developed out of proportion to the base; the yolk-bag has disappeared; the gill-cover extends, when pressed against the sides (Plate III. fig. 31), well up along the base of the pectorals; they are now kept in constant rapid motion, so that the fleshy edge is invisible, and the vibration seems almost involuntary, producing a constant current round the opening leading into the cavity of the gills. The latter are seen now to branch quite extensively. The extremity of the tail also has the same rapid vibratile motion which characterizes the pectorals. Professor Agassiz had already noticed this rapid involuntary movement in the temporary caudal lobe of a young Lepidosteus about eight inches in length.

In the stages intervening between Plate III. fig. 19, and Plate III. fig. 30, the young Lepidosteus frequently swim about, and become readily separated from their point of attachment. In the stage of Plate III. fig. 30, they remain often perfectly quiet, close to the sur-
face of the water; but, when disturbed, move very rapidly about through the water. In this stage, we can notice the first trace of the ventrals, at the anterior part of the ventral embryonic fold. They appear first as minute swellings on each side of this fold, and they consist of a central shaft with a fleshy fringe like the pectorals. Seen from above (Plate III. fig. 32), the head has become elongated, the sucking-disk is reduced to a single row of small suckers, and we now begin to see what becomes of this organ. The fleshy globular termination of the upper jaw of the adult Lepidosteus is the remnant of this embryonic sucking-disk. The coloring of the young fish is becoming more and more like that of the adult; the dorsal region is mottled with broad irregular patches of brown; a strong black line extends from behind the eye, on the lower side of the median line, to the extremity of the tail. The young already have also the peculiar habit of the adult of coming to the surface to swallow air. When they go through the process under water of discharging air again, they open their jaws wide, and spread their gill-cover, and swallow as if they were choking, making violent efforts, until a minute bubble of air has become liberated, when they remain quiet again. The resemblance to a Sturgeon in the general appearance of this stage of the young Lepidosteus (Plate III. fig. 30) is quite marked.

The growth of the young Lepidosteus is very rapid. Hatched the 28th of May, they had on the 14th of June attained a length of threequarters of an inch (Plate III. fig. 33). The snout has become greatly elongated; and the upper jaw shows plainly that the sucking-disk is to become the fleshy accretion at the extremity of the snout. The embryonic fin-fold has become slightly indented, indicating the positions of the future dorsal and anal fins. The ventrals have increased somewhat in size. In this stage, we see the first trace of the permanent fin-rays, of the dorsal, caudal, and anal fins. There are also most delicate embryonic fin-rays, just as we find them in bony fishes at corresponding stages. The fringe of the pectorals is incessantly in rapid vibration, as well as the tip of the tail, except when the fish is at rest near the surface of the water. The tail does not necessarily vibrate with the pectorals: either may be in motion without affecting the other. The teeth make their appearance in this stage, and there are a few fin-rays in the fringe of the pectorals.

Seen from above, the pectorals are usually carried at right angles to the body when in rapid motion (Plate IV. fig. 34). Our young Lepidosteus has now reached a stage (Plate IV. fig. 36) very similar to that first described by Professor Wilder. The head, when seen from
above, shows the sucking-disks reduced to a couple of rows of independent suckers, but the young Lepidosteus no longer attach themselves by it. They have assumed the habits of the adult, rising slowly near the surface, where they frequently remain almost motionless for a long time, merely keeping the pectorals and the tip of the tail in rapid vibration. When they wish to swim about, they strike out vigorously with their tail-fin laterally.

When in a natural attitude, they float with the body curved, the back behind the head flush with the surface, the head nearly horizontal, and the tail curved down (Plate IV. fig. 39, Plate V.).

By the 22d of June, the anterior part of the head had elongated, and the indentations of the embryonic fin-fold marking the future fins are deeper; but the embryonic caudal is still by far the more prominent of the two caudals, although the fin-rays of the permanent caudal are well laid out, and its position has become more terminal than in previous stages (Plate IV. fig. 38).

The external changes undergone by the young Lepidosteus, until the last one of them hatched at Cambridge died, were limited, in the anterior part of the body, to the greater elongation of the jaws; the increase in size and number of the teeth (Plate IV. fig. 41); the growth of ventrals, which resemble in their structure that of the pectorals (Plate IV. fig. $41 a$ ) ; and, in the posterior part of the body, to the better definition of the shape and position of the dorsal, anal, and caudal, as well as the great apparent increase in the length of the temporary caudal filament, from the gradual resorption of the posterior embryonic fin-fold. The head of the young Lepidosteus now shows no further trace of the sucking-disk beyond the fleshy swollen termination of the upper jaw.

There are in this stage five gill-arches carrying short lateral branches (Plate IV. fig. 43). Seen from below, the gill-covers unite on the median line, immediately at the base of the lower jaw.

The largest specimen grew to a length of $\mathrm{t} \frac{5}{6}$ of an inch, and its coloring (Plate V.) did not differ from that of larger young specimens denoted by Professor Agassiz, which had already attained a length of eight inches.

In conclusion, we may say, as a result of the above observations on the external development of the Lepidosteus, that, notwithstanding its similarity to Sturgeons in certain stages of its growth, notwithstanding its affinity with Sharks and Skates, by the formation of the pectorals from a lateral fold, as well as by the mode of growth of the gillopening and the gill-arches, the Lepidosteus is, spite of all this, not
so far removed from the bony fishes as has been supposed. On the contrary, it approaches them not only by the development of the general features characterizing the posterior extremity, by the mode of formation of the unpaired fins from the embryonic fin-fold, by the mode of formation of the fin-rays, and also by that of the ventrals. The pigment cells, so well developed in their young stages, before the appearance of scales, are similar to those of bony fishes, with the exception that we have in addition, in early stages, cells of a white silvery lustre, which are undoubtedly the first trace of the enamel to form the armor of the "Garpike."

## EXPLANATION OF THE PLATES.

## PLATE I.

Fig. 1. Young Lepidosteus just escaped from the egy, measuring $8^{\mathrm{mm} .}$ in length.
2. Tail of specimen slightly older.
3. Tail of specimen somewhat older than fig. 2.
4. Head of young Lepidosteus just hatched, showing the mouth cavity and the disk.
$4 a$. The same, seen somewhat more in profile.
5. Another specimen, with the head thrown back, looking into the mouth cavity.
6. Head seen in profile, showing the gill-arches, the heart, the auditory capsule, and the muscular segment covering the chorda.
7. In stage of fig. 1 (hatched the same day), seen from ahove.
8. Head of specimen somewhat older than fig. 7.
9. Gill-arches of specimen in stage of fig. 7.
10. Shows position of heart in middle of anterior part of the yolk-bag.
11. Young Lepidosteus at the end of the first day.

## PLATE II.

12. Young Lepidosteus, seen from above, three days old.
13. Same, seen in profile.
14. Profile of young on the fifth day after hatching.
15. Same as fig. 14 , seen from above.
16. Gill-openings of same specimen.
17. Same age as fig. 14 , seen from the lower side.
18. Anterior part of young Lepidosteus, ten days old, seen from below.

## PLATE III.

Fig. 19. Profile of young specimen eleven days old.
, 20. Head of same, seen from above.
" 21. Magnified pectoral of same.
" 22. End-view of sucking-disk of same.
", 23. Profile of head of specimen somewhat more advanced.
"24. Profile of sucking-disk of another specimen about in the same stage of development.
25. Tail of specimen of same age as fig. 19, but somewhat more advanced.
26. Gill-opening of same, seen from above.

Figs. 27, 28. Profiles to show protuberances of sucking-disk of head in different degrees of expansion, one day older than preceding stage.
Fig. 29. Profile of head of specimen thirteen days old.
30. Profile of young Lepidosteus $20^{\mathrm{mm}}$. long, nineteen days old.
," 31. Head of same, seen from above.
„32. Tail of specimen seventeen days old, but evidently more advanced than the preceding figure (30).
33. Head of same (fig. 32), seen in profile. The young specimen measured $20^{\mathrm{mm}}$ in length.

## PLATE IV.

Fig. 34. Young Lepidosteus, twenty days old, slightly larger than the stage of the previous day, seen from above.
35. Tail of same, seen in profile.
36. Profile of young, $21^{\mathrm{mm}}$ in length, twenty-four days old.
37. Head of same, seen from above.
38. Young, seen in profile, twenty-five days old.

38a. Profile of tail of same, showing commencement of fin-rays of caudal, anal, and dorsal fins.
39. Natural attitude of young Lepidosteus, thirty days old, seen in profile, $\frac{15}{15}$ of an inch long.
40. Tail of young Lepidosteus, thirty-eight days old, of about the same length as the specimen of fig. 39.
40a. Pectoral of same.
41. Profile of jaws of same.

41a. Commencement of ventrals of same.
42. Head of same, seen from above.
43. Gills of same, in profile.
44. Gills and gill-arches, seen from below.

## PLATE V.

Natural attitude of young Lepidosteus (early part of July) after it has assumed to a great measure the coloring of much older specimens. This specimen measured about an inch in length.

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