Some Remarkable Shells of a South American Fresh-Water Mussel

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In November, 1943, Chicago Natural History Museum received, as a gift from the Chicago Brazilian Consulate, a small collection of fresh-water shells, and among these were some striking specimens of what doubtless is *Anodontites (Lamproscapha) ensiformis* Spix. Unfortunately, no exact information of the locality or localities was given, for the statement "Brazil" does not mean very much to modern taxonomy; but from some of the accompanying species as well as from the botanical specimens received at the same time from the same source, it is certainly probable that the entire material came from the region of the lower Amazon. The fact that the collections in question had originally been part of a display showing Brazilian natural products of economic importance, in which the shells involved represented the raw material of button manufacture, corroborates this assumption, since only localities close to the mouth of the Amazon, close to a center of industry or exportation, could produce shells for this purpose to compete on the world market.

Though reported from the Amazon River in general by preceding authors, *Anodontites ensiformis* has never been reported from a definite locality within the basin of the lower Amazon. A compilation of our knowledge of the species in question may be found in Ortmann (1921, pp. 630–632), who corrects the somewhat misleading statement of Simpson (1900, p. 932; 1914, p. 1455) that *ensiformis* is distributed over "Tropical South America" to the proper limits, i.e., the system of the Amazon. We do not find, however, in the compilation mentioned, any record of the species from the lower Amazon.

It is noteworthy that the original locality of *Anodon ensiformis*, which was not expressly stated by its author, may have been within the lower Amazon region, though von Ihering (1890, p. 161), in his

revision of the Spixian naiads from Brazil, makes the somewhat dubious statement that the type probably came from one of the tributaries of the upper river. If we trace Spix's route in Brazil, we see that he ascended the Amazon from Belem in the east to Tabatinga in the west, i.e., from the very lower part to well into the upper one. Thus the evidences for lower and upper Amazon as type localities of *ensiformis* are equal and no reasonable conclusion in favor of one of them can be drawn from the author's route; we shall see later that the picture given by Spix may reveal some decisive factor.

As before said, our specimens, though here considered to have originated in the lower Amazon, cannot give final proof of the supposition that *Anodontites ensiformis* is present in the lower Amazon or in such of its tributaries as the Ríos Tapajoz, Xingú, and Tocantins, but some of the features of the 50-odd valves under consideration (C.N.H.M. No. 19416) plainly point to localities in which life conditions are almost optimal, i.e., in which there is no strong current, no appreciable seasonal change of the water temperature, plenty of food, and a deep, soft mud on the bottom, a combination of ecological factors not to be expected in the upper Amazon. The features indicated are first of all the size attained, and secondly the change of outline in the course of the shell growth.

The fact is well established that the species of fresh-water bivalves inhabiting a river throughout its course are smallest in its headwaters, larger in the middle portion, and largest in its lower course. The reason for the smaller size of headwater specimens of rivers is not only the relative smallness of the water volume in which they live, as some authors have assumed, but also the more or less torrential character or at least rapid current of most of such headwaters. When a river in its middle course crosses a mountainous region and thus reacquires a stronger current and a bed of coarser pebbles—in other words, where it reassumes torrential features—its bivalves show a somewhat reduced size and other characters pointing toward life conditions similar to those in the river's headwaters. Such a case, in Europe, is found in the Rhine, when, after a rather long course in a broad, quiet valley, it breaks through the Schiefergebirge in a winding, narrow gorge. Analogous conditions prevail in the upper Amazon and its headwaters, which are all already mighty rivers, but which nevertheless still offer torrential life conditions, that only in very rare and exceptional cases permit maximum growth in the bivalves present. This seems to be supported by the fact that all the known upper Amazonian *ensiformis* are of rather reduced

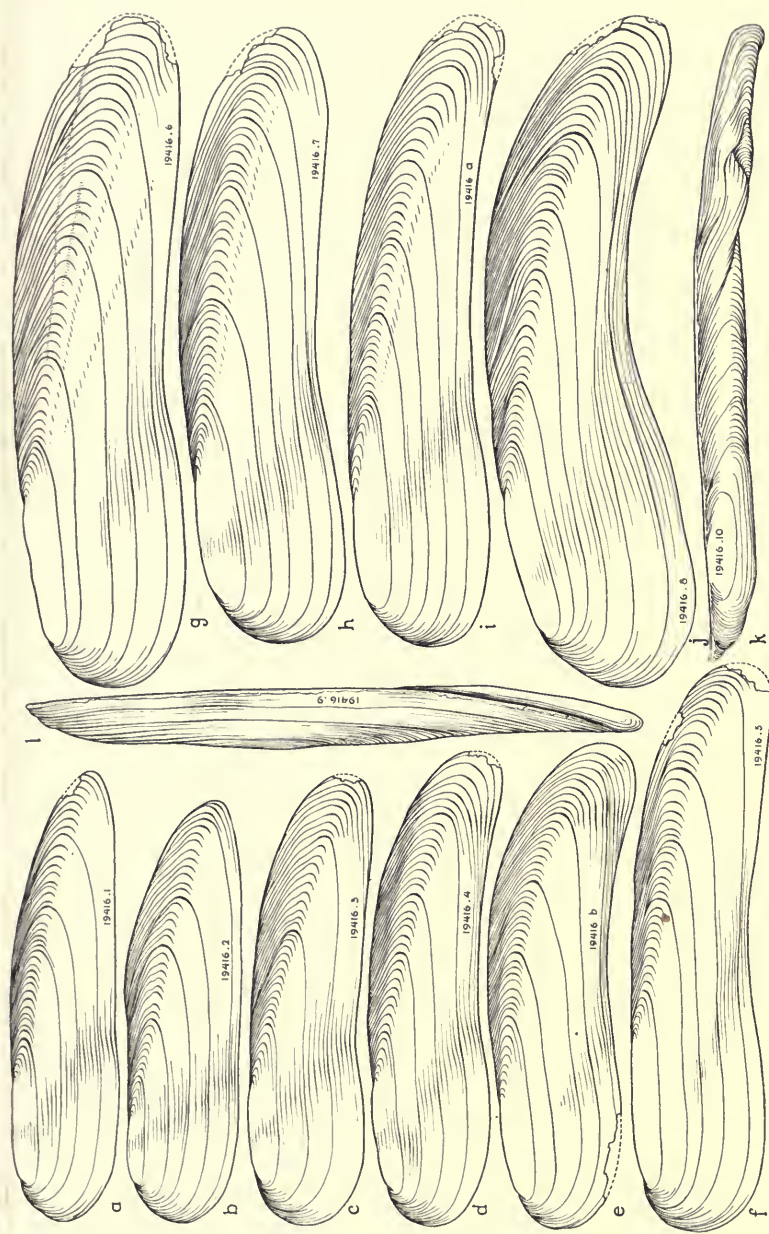Fig. 3. Growth rings on valves of *Anodontites* (*Lamproscapha*) *ensiformis* Spix. C.N.H.M. No. 19416. *a–j*, from right side; × 0.5. *k*, from above; *l*, from below; × 0.5.

size.   Ortmann's list of measurements shows this plainly.   The longest specimen then known was one recorded by Orbigny from Bolivia (Río Itonoma, a tributary of Río Guaporé, in turn a tributary of the Mamoré, all of the upper Amazon Basin).   This specimen measured 130 mm. in length, while the longest specimen Simpson had seen measured only 106 mm.   Ortmann did not include the measurements of the "Brazilian" specimens figured by Spix (Wagner, 1828, p. 31, pl. 29, figs. 1, 2) and by Küster (1838, p. 8, pl. 2, fig. 2), both of which measure 129 mm.; and my own record (Haas, 1931, p. 102) of a specimen of *ensiformis* from "Brazil" 128 mm. long was a subsequent one.   In my records of large freshwater mussels (Haas, 1941), *Anodontites ensiformis* was not mentioned at all.

In contrast to these measurements of *ensiformis*, part of which undoubtedly refer to upper Amazonian specimens, the average length of our supposedly lower Amazonian specimens of lot 19416 is 160 mm., while about a third of them attain much greater length, with a maximum of 196 mm.! The discrepancy between the preceding measurements and mine, together with some other shell features to be discussed below, supports my assumption of a provenience from localities situated in the lower Amazon system.

The shell features that seem to indicate provenience from the lower course are clearly shown in figure 3.   Figure 3, *a* and *b*, apparently represents typical specimens of *ensiformis*, with its characteristic pointed posterior end; on closer inspection, they are seen to differ from upper river specimens by being flatter, and by their much smoother, darker, and dull-colored outer surfaces; furthermore, these two shells are doubtless immature, whereas specimens of equal length found in the headwaters of the Amazon are apparently full-grown.   At any rate, I assume this to be the case, from the lack of larger specimens from these regions.

From ecological experience, the differences mentioned in the shell features point to basically different biotopes, in which the respective phases of *ensiformis* live.   The more inflated and slightly thicker-shelled headwater phase, with its close-set and rather pronounced growth marks, and with a constant shade of dark green, mostly in the umbonal region, but occasionally also on lower parts of its otherwise chestnut brown cuticle, lives in such rapidly moving water that the deposition of mud or even of fine sand on the bottom is impossible; coarse pebbles or even small rocks will be the ambient in which such bivalves have to live and grow.   Flat shells are in

danger of being crushed by the constantly shifting stones, whereas a degree of curvature, according to the rules of statics, adds to their resistance; this accounts for the somewhat greater inflation of the headwater shells, while the lack of humic acids in the water determines the brighter colors of the cuticle. Their much more crowded growth marks are presumably the result of seasonal changes of life conditions in the water, such as reduced food supply or a sensible fall of temperature, or a combination of both factors, by which the metabolism of the bivalve is reduced, with temporary suspension of the shell growth; the cooling of the water by the annual summer melting of snow and ice in the high Andes may have the specified effect. As a final consequence, more difficult life conditions in the Amazon headwaters apparently stop the growth of *Anodontites ensiformis* at a shell length of about 130 mm., at which length the shell has not undergone any striking changes of shape, preserving the original pointed, sword-like outline.

Returning to the features of shells *a* and *b* of figure 3, these shells must come from a biotope very unlike that of the swifter river. The flatter and, to a certain degree also thinner, shell in these specimens must have grown in a quiet water environment, in which the danger of being crushed was absent, and where favorable life conditions must have prevailed throughout the year, thus permitting uninterrupted growth of the shell, as indicated by its smooth outer surface and by the fainter and more widely spaced growth marks. The dull earth-brown color of the cuticle must be associated with a thick layer of mud on the bottom of the water, in which the shells were almost entirely buried. These features point to a sluggish lower course of a river or to a bayou more or less separate from the main river—in other words, to an almost stagnant or completely stagnant body of water. Though such nearly optimal life conditions may exist in some quiet backwater in the upper course of the Amazon, it is not likely that the shells under consideration came from such a one, in view of the accompanying typically lower-Amazonian shells and botanical objects, as well as in view of the economic factor mentioned.

Among the comparatively few illustrations of *ensiformis*, that given by Chenu (1859, **2**, p. 146, fig. 721) can be disregarded since it is too much schematized to reveal any details about its life history. Orbigny's figure (1843, p. 618, pl. 79, fig. 10) shows only the outlines of a right valve with the soft body in it, but the corresponding text shows that an upper river specimen served as the original. Of the remaining three illustrations, that of Sowerby (1867, pl. 11, fig. 31) shows a very young specimen of unknown locality in Brazil, but

from the description of the coloration it is clear that the bright olive green of the anterior side points to a locality in the headwaters of the Amazon.   The two remaining figures are those of Spix (Wagner, 1828, pl. 24, figs. 1, 2) and of Küster (1838, pl. 2, fig. 2).   These agree in representing specimens of a rather dull brown color, and this suggests a provenience from muddy and perhaps stagnant water—in other words, from the lower course of the Amazon.   Küster merely repeated Wagner's Latin description in German with the identical measurements, and figured the identical specimen that had served as original for Spix.   Spix's figure is the less accurate of the two, since it represents the left valve in a rather oblique view, thus somewhat distorting its outline and showing the dorsal portion of the right valve.   Küster avoided this inexact view by providing an undistorted vertical view of the left valve; nevertheless the two figures agree so well that a tracing of Spix's figure almost exactly overlaps that given by Küster.   Küster lived and worked in the small Bavarian university city of Erlangen, and I know that the shell collection of Munich (which includes the Spix collection) was made available to him and to others for monographs in the Conchylien Cabinet.   These two existing figures of the type of *ensiformis* agree in showing it to be a dull brown-colored shell, suggestive of an origin in quiet or stagnant water.   Spix, in addition, gives an internal view of both valves, and these, though rather imperfect as to technique, suggest a certain flatness of the valves and a shallowness of the umbonal cavities found again in our supposedly lower river specimens of *ensiformis*.   The figures of the type accordingly support my assumption that the original locality of the species was in the lower Amazon.

Extending our study to the larger specimens of the lot in question, we return to the assumption that their larger size indicates origin from the lower Amazon.   This interpretation is supported by my records of large fresh-water mussels (Haas, 1941).   Quoting only those that refer to quiet water or pond occurrences of otherwise fluviatile species necessitates the omission of tropical and North American examples, in which the biotope is not stated.   The relatively few cases left speak for themselves.   In the following list there is no doubt that the attainment of unusual size is restricted to sheltered localities, to suboptimal or optimal life conditions in backwaters, bayous, ponds, or the sluggish waters of slowly flowing lower courses of rivers: *Aspatharia petersi* Martens, *Anodonta cygnea* Linnaeus, *Unio crassus crassus* Retzius, *Unio crassus cytherea* Küster, *Unio pictorum pictorum* Linnaeus, *Unio pictorum latirostris*

Küster, *Unio pictorum platyrhynchus* Rossmaessler, and *Unio tumidus tumidus* Retzius.   In these cases the excessive growth of length, as distinguished from the fluviatile phase, is clear, though it amounts only to some 30 mm. as a maximum.   In the case of our assumedly lower Amazonian *ensiformis* the difference reaches 67 mm.   There cannot be any doubt that our specimens of *ensiformis* are really much longer than the hitherto known fluviatile phase of the species. From the combination of theoretical considerations with the examples listed, I conclude that both our specimens and the Spixian type came from the lower Amazon.

The statement that maximal sizes are generally only attained in quiet, almost stagnant waters, though correct in itself, needs some further discussion.   In the expression "maximal" or "unusual" or even "record" sizes no distinction is made between normal growth equally involving all three dimensions of the shell, and excessive growth in length with resulting disproportion between the length and the two other dimensions.   Uniform growth in all three dimensions is really the result of the best life conditions conceivable, in the truly optimal environment, if such a condition is possible.   Bivalves of maximal size showing a proportionate increase in length, width, and height of shell do not originate in muddy waters, or exclusively in stagnant waters.   As far as I know, such maximal unionids were all found in the fine, deep, and only slowly shifting sand at the bottom of slowly moving rivers, whereas anodontids attain their proportionate maximal development in clear ponds with a bottom of a soft clay and not of loose mud.

Maximal size accompanied by disproportionate length of the shell, on the other hand, is the result of life in sheltered and almost optimal waters, whose bottom consists of a more or less deep layer of mud.   Such waters offer almost as good life conditions as the sandy habitats of large unionids and anodontids, in which there is no disproportionate growth; in some respects the environment is even more favorable since certain dangers such as the result of seasonal changes in current conditions are absent.   On the other hand, the mud bottom influences the shells inhabiting them to react by a differential growth of shell proportions.   The layer of mud on the bottom occasionally endangers the mollusk.   If this layer is thin and spread over a base of sand or fine gravel, as is often the case in backwaters of rivers cut off from the main course, its influence on the shape of shells is negligible. The effect on the color of the cuticle is obvious, for those portions that stick out of the sand underneath and are imbedded in the mud above it are colored dull brown or even black, while the portion in

the sand retains the original light, yellow, greenish-yellow, or green color of the cuticle. When the layer of mud is as deep or deeper than the average length of the bivalve shell, its basal part generally is sufficiently dense to permit the shells to stay there without sinking to the harder bottom of sand or pebbles or whatever its nature. In such a case, the entire shell will show the dark, lusterless discoloration. This, by the way, can mostly be removed by treatment with rather diluted mineral acid, such as hydrochloric, and the original brighter color of the cuticle will be restored.

In these cases the mud still acts as a protecting agent, hiding and sheltering the shells from adverse outside factors such as currents, surf, or even predators. As soon as the bottom layer of mud becomes deeper than the length of a shell, it becomes a real peril to the animal, since it covers the posterior end where the inhalant opening is situated, endangering the breathing process. As long as the mud is still very thin, the danger of suffocation is not imminent; but when the mud layer attains a considerable depth, the shell by its own weight will sink out of the reach of the necessary oxygen supply. In this case the conditions become unfavorable. Except to leave the spot of such danger and emigrate to another where the conditions for breathing are better, the only means left to avoid danger of being suffocated lies in the elongation of the posterior end of the body, and, correspondingly, of the shell, with the effect of keeping the respiratory openings within the open water or, at least, within the thin, breathable upper layer of the mud. Since only a very restricted number of bivalves can emigrate from the suffocating mud layer, the majority is driven to the latter alternative. In deep mud habitats, the thickness of the bottom mud generally does not change suddenly, so that the environment is relatively constant and the bivalves can meet slow change by slow growth in length. Thus the prolongation of the posterior end compensates the slow sinking into the mud. Of course this process will take place at a lesser depth of mud in smaller species than in larger ones.

No experiments have been made to corroborate the ideas just expressed; but we can point to experiments made by nature. When we compare specimens of certain species of *Anodonta* and *Unio*, from ponds and swamps, with others collected in open lakes and rivers, we see that the former are mostly larger than those of the latter habitats, and that this excess of size is mostly contributed by posterior elongation. Figures in monographic works on fresh-water shells, or in illustrated faunas, exhibit these mud-bottom types. For

simplicity I mention only two works, though examples might be found in almost every publication on Unionidae and Mutelidae:

Anodonta cygnea Linnaeus (as *cariosa* Küster); Küster and Clessin, 1853, pl. 5, fig. 1, pl. 10, figs. 1, 2.

Anodonta cygnea Linnaeus (as *diminuata* Clessin); Küster and Clessin, 1876, pl. 87, fig. 1.

Anodonta cygnea Linnaeus (as *rostrata* Rossmaessler); Rossmaessler and Kobelt, 1842, pl. 54, fig. 737.

Microcondylaea compressa Menke (as *squamosa* Drouet); Kobelt, 1913, **19,** pl. 636, figs. 2756, 2757.

Unio pictorum proëchus Bourguignat; Kobelt, 1911, **17,** pl. 463, figs. 2498–2500.

The disproportionate growth in length shown in these examples, and shown also in our valves of *Anodontites ensiformis,* necessarily changes the entire aspect of the shells affected; the change is most obvious in the relative position of the beaks in young and in old shells, for these will naturally shift proportionately toward the anterior end as the posterior end grows in relative length. Such a relative forward shift of the beaks takes place during the growth of every fresh-water mussel, the position of the umbos being, in the youngest shells, always much more central than in older and in full-grown specimens. This fact, known to every student of Unionidae and Mutelidae, is due to a normal, though slight, disproportionate growth of the rear end of the shell. It becomes much more emphasized and noticeable when life conditions like those of the mud habitat just described prevail. Thus in *Anodontites ensiformis* from upper river habitats there is a relative movement of the beak toward the anterior end, as can be seen in the following table from Ortmann (1921, p. 632):

Locality	Length	Beaks
Río Machupo, Bolivia (at San Joaquin)	35 mm.	At 9 mm. = 26% of length
	50 mm.	At 10 mm. = 20% of length
	55 mm.	At 11 mm. = 20% of length
	52 mm.	At 10 mm. = 19% of length
"Brazil"	78 mm.	At 14 mm. = 18% of length
Río Itonoma, Bolivia	130 mm.	15% of length

This relative shift of beak position becomes insignificant in shells from hard bottoms. It continues in shells of greater length in the series from our assumedly lower Amazonian specimens:

Catalogue numbers	Length	Beaks
19416.1	132 mm.	At 15.5 mm. = 15.5% of length
19416.2	123 mm.	At 14.4 mm. = 11.7% of length
19416.3	132 mm.	At 16 mm. = 12.1% of length
19416.5	169 mm.	At 19 mm. = 11.2% of length
19416.7	180 mm.	At 21.5 mm. = 11.9% of length
19416.8	197 mm.	At 27 mm. = 13.9% of length

The figures given in this table are not exact, since in older shells it is impossible to indicate the exact position of the beak; but approximate as they are, they still clearly show the progressive forward shift of the beak.

So far, I have only discussed the excessive prolongation of the posterior end of naiad shells in general, and of *Anodontites ensiformis* in particular, as a reaction against bogging down and suffocating in mud bottom. This counteraction by an organism of unfavorable environmental conditions is purely an ecological process; but the phenomenon in question is obviously more complicated, as may be seen when the outlines of our *ensiformis* specimens in different stages of growth are compared in figure 3, *a–j*. In these figures a progressive tendency toward broadening of the posterior end may be seen, so that the longest valves appear broadly truncated, very much in contrast with the younger shells, which have a pointed rear end. Young and half-grown shells differ so much from full-grown ones that they really look like different species. The gradual change from pointed to pointless in intermediate stages (fig. 3, *c–d*), and the course of the earlier growth-marks in the old shells, which represent the change of shape undergone in one and the same individual (fig. 3, *e–j*), link the extremes together, proving that they represent a single species, namely, *ensiformis*.

Such broadening of the extreme posterior end is known in many other naiads and is to be discerned in almost all cases of lengthening the rear part of the shell in the presence of deep, thin mud. *Anodontites ensiformis* illustrates the extreme combination of lengthening and widening of the posterior part of the shell.

I have been unable to connect this broadening of the rear end with any possible reaction of the mollusk to improve its condition in the mud-bottom environment, with which this broadening invariably seems to be correlated. Since the truncation of older *Anodontites ensiformis* apparently has no direct relation to life in quiet water, it does not bear on my assumption that these shells had come from the lower Amazon. A more remote and indirect relation may be seen in the architectural rules governing shell construction in general.

The rear end of the naiad shell in general, and its excessively elongated portion in particular, are much thinner than the anterior end. This condition (possibly connected with the necessity of rendering the whole shell as light as possible) produces a pointed, narrow end that is weak and liable to crack. When this end is broad, though as thin as before, this danger will be reduced. If this assumption is correct, the broad end of the shell is not part of the direct adaptive process counteracting adverse environmental conditions, but a part of the unknown and mysterious mechanisms that govern the structural aspect of shell formation.

All slender and pointed fresh-water shells become at least somewhat less pointed during their growth to the adult stage. The smaller species, which are relatively protected throughout life, do not show this very clearly; for example, the European *Unio pictorum* Linnaeus and *Unio tumidus* Retzius and the North American species of the group of *Elliptio jayanus* Lea. To support my ideas about *Anodontites ensiformis* it is necessary to look for shells equally or similarly long, slender and pointed, but since *ensiformis* represents almost the extreme of slenderness and pointedness in naiads, it is difficult to supply further examples.

One East Asiatic species, *Lanceolaria grayana* Lea, is almost identical with *ensiformis* as far as the general shape is concerned; I was able to figure the largest specimens known (Haas, 1910b, p. 44, pl. 2, figs. 1–5). These specimens seem to have come from quiet water, but apparently not from a muddy environment; they exhibit an almost optimal development, with very little, if any, excessive posterior prolongation, and their rear extremity is almost as pointed as in very young shells. Another species, *Lanceolaria triformis* Heude, though not as slender and as sharply pointed as *Anodontites ensiformis*, offers a greater analogy to *ensiformis* than does *L. grayana;* as may be seen from my figure (Haas, 1910b, p. 49, pl. 3, figs. 3–5), this species begins as a posteriorly pointed shell, but during life it changes its shape by developing a broad, truncated rear end. This *Lanceolaria triformis* will have to be mentioned again in another connection.

Other long, slender naiads with a shell constitution and length comparable to those of *Anodontites ensiformis* are the species of the neotropical genus *Mycetopoda* and of the Asiatic genus *Solenaia*, all of which are almost of the shape of a leguminous pod; but none of them, even in the youngest stages known, is ever pointed posteriorly, all being truncate at the rear end. Thus they do not afford comparison with the Amazonian form. The North American *Elliptio*

shepardianus Lea is a naiad comparable with *Anodontites ensiformis* in general aspect of the shell and in the corresponding broadening of the posterior end during growth. Though I have no young specimens at hand, older ones reveal the juvenile pointed shape by the course of their growth marks. Unfortunately nothing is known to me about the life habits of this striking species, so that its shell features are unexplained. The larger specimens of *Anodontites* present another feature that is known only in limnic phases of naiads and therefore suggests quietly flowing channels of a lower river course and the lake-like bayous as their place of origin. I allude to the very obvious, hook-like form of the rear ends of some of the shells (fig. 3, *e, h–j*), the decurvation (as Rossmaessler termed it), which makes the rear-most portion of the shell so strikingly rostrate. Rossmaessler (Rossmaessler and Kobelt, 1844, **2**, pt. 6, pp. 1–25) was the first to describe and to understand this strange phenomenon. He showed that it is not a specific character but an ecological one due to environmental conditions. His only form exhibiting decurvation came from Lake Wörther in Carinthia. Subsequent collectors found corresponding phases of unionids, of other species as well as of *pictorum*, to which Rossmaessler's classical example, *Unio platyrhynchus*, belongs, in many other lakes or limnic water bodies in central Europe (see Küster, Borcherding, Haas and others), and in comparable, though not as accentuated cases also in African lakes (Haas, 1936, p. 58, pl. 5, fig. 1, *n–o*). While there is no doubt about the exclusive origin of decurvation under lacustrine condition, no satisfying explanation has been found for it; those offered are listed by myself (1910a, pp. 164–167).

The decurvation shown in some of our specimens of *ensiformis* is as typical and as highly developed as in *Unio platyrhynchus* Rossmaessler, which presents the best example of this feature. Since not all our valves of *Anodontites ensiformis* show the decurvation at an equal degree, it may be assumed that they were collected in various localities, of which only a few or only one offered the lacustrine conditions indispensable for the development of a decurvated rear end; other shell features had already led me to the belief that the lot of *ensiformis* shells received together had not originated in a single, ecologically clearly circumscribed biotope. Some of these shells, namely the non-decurved ones, may be of fluviatile origin, while the remainder, which exhibit decurvation, are of lacustrine origin. A possible objection, that isolated ox-bow lakes are not true lakes and that pronounced limnic action on the shells living in them can not be expected, may be countered by the fact that a typically decurved

phase of *Unio tumidus* Retzius was discovered by me (Haas, 1910a, pp. 163–167, text figs. 7–12, pl. 14, fig. 10) in a backwater of the Rhine severed from the main river for many decades. Ox-bows and bayous of the lower Amazon that have lost their connection with the open river may, on account of their doubtless much greater area, be still more likely to develop lacustrine conditions.

In this connection, we may discuss some features not attributable to direct influence of the surrounding medium that alter the shape of the shells in question. There is, first, the tendency even in the straightest specimens to curve in the ventral margin (see fig. 3, *a–j*); slight as this sinuation is, it is rather general, not only in *Anodontites ensiformis*, but in most naiads with a straight ventral margin. This becomes clear from examples to be found in collections and published illustrations, and from the figures cited above referring to the prolongation of the rear end. The bending in of the ventral margin we are discussing now cannot be regarded as a merely accidental deviation from straight growth; if it were such, the reason why no deviation to the other side ever takes place would remain obscure.

I am, therefore, inclined to regard the in-bending of the ventral margin as a means of stiffening the shell's structure; this curvature is thus not comparable to the decurvation of the posterior end. This structurally conditioned inward curving of the middle ventral margin apparently develops when some strengthening of the shell is needed to counteract the weakening effect of the broadening and decurvation of its rather thin and flat extreme rear end. This counteraction against breakage of the rostrate posterior end is effected by a striking inflation of the shell all along its posterior ridge and by a corresponding depression and sinuosity of its central portion. The North American fauna offers an example of such a reaction in *Gonidea angulata* Lea, though on a smaller scale than in *Anodontites ensiformis*. Since the shell is stiffened by the development of a central swelling, acting as a supporting beam, the normal tendency of the shell to slight curvature of the middle ventral margin comes to meet the need of a structural strengthening of the shell, and accordingly the curvature becomes much more accentuated. The whole process results in a convexity secondarily added to the originally flat shell, that gives it a greater resistance to external stress.

As has been shown, change of shape of the shell, correlated with environmental factors, involves complex compensatory changes in the structure of the shell. Actually there are almost always irregularities in shells that have undergone such change. The two valves of a single shell may differ in convexity, or in height, or they may be

slightly distorted by deviation from the axis of bilateral symmetry, or they may differ in all these respects. In some cases such deviations become so striking that the shells in question look quite abnormal, especially if lateral deviation from the axis of symmetry is combined with torsion. In some oriental unionids this feature is genetically fixed as either a generic or a specific character: generic in the genera *Arconaia* and *Cuneopsis*, specific in some species of *Arcidopsis* and of *Lanceolaria*. In connection with this deviation the Chinese naiad *Lanceolaria triformis*, mentioned above as an example of an originally pointed species becoming broad behind during the period of growth, should be mentioned again, since, exactly as in *Anodontites ensiformis*, it combines this broadening with deviation. Figure 3, *k* and *l*, shows that, in the Amazonian shell, valves that exhibit decurvation of the rear end and compensatory inflation of the disk, develop such lateral distortion.

These distortions are probably the unexpected results of an imperfectly working compensatory mechanism and as such they have no bearing on our biotopic problem; for they become evident in other compensatory changes of shape due to different reasons.

A relative of *Anodontites ensiformis*, also of the subgenus *Lamproscapha*, has been described under the name *falsus* (Simpson, 1900, p. 932; 1914, p. 1456) as having a broad, rounded rear end; the locality is the Yuruari River, in Guyana, a tributary of the Essequibo (see Ortmann, 1921, p. 630). I have been tempted to correlate our broad phase of *ensiformis* with *Anodontites falsus*, but knowing *falsus* only from the description, Simpson's statement that *falsus* at a length of only 77 mm. already has such a truncated and broadly rounded rear end, indicates that it differs radically from our *ensiformis*, which at this length have the original pointed posterior end. It is, therefore, advisable to recognize two different species of the subgenus *Lamproscapha*, the Amazonian *ensiformis* Spix, and the Essequibo *falsus* Simpson. The latter form may extend into the Orinoco system.

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