CORRELATION BETWEEN THE DISPOSITION OF THE LIVER AND THE KIDNEY AND THE FORM OF THE AIR-BLADDER IN CERTAIN SILUROID FISHES OF INDIA.[1]

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Several workers have observed and commented upon the peculiar disposition of the liver and the kidneys in certain Siluroid genera, such as *Plotosus* Cuv. & Val., *Heteropneustes* Müller (=*Saccobranchus* Cuv. & Val.), *Clarias* Linn. and *Heterobranchus* Geoffr., but, so far as I am aware, no satisfactory explanation for this peculiarity has yet been advanced. Dutta (1924), who reviewed the whole subject not very long ago, came to the conclusion that

> 'This unusual position of the liver and the kidney can be regarded with a very fair amount of probability to be due to the smallness of the body-cavity in which the comparatively larger liver and kidney do not find enough space and are thus thrust outside.'

Weber (1891) had previously suggested that the peculiar disposition of the liver and the kidneys in *Clarias* and *Heterobranchus* was due to the lateral expansion of the air-bladder, which carries sideways with it small lobes of the liver and the kidneys.

It is unfortunate that Bridge and Haddon's (1893) very illuminating remarks concerning the peculiarities in the disposition of the liver in certain Siluroid fishes and its correlation with the form of the air-bladder should have escaped the attention of all recent workers on the subject. According to these authors the outwardly directed peritoneal cul-de-sacs were developed for the reception of the lateral lobes of the liver as a result of the unusual lateral extension of the anterior chamber of the air-bladder and its apposition on each side to the external skin. They further stated (p. 296) that

> 'The possibility, however remote, that these anatomical features have no special physiological value, but are simply the necessary result of other structural modifications of undoubted utility, must also be kept in view. The relative shortness of the abdominal cavity in many Siluroids may have caused the lateral extension of the air-bladder and its consequent abutment against the external skin.'

Recently in connection with my work on the Siluroid fishes of India for a revised edition of 'Fishes' in the *Fauna of British India* series, I dissected a large number of specimens belonging to different genera of Indian Catfishes for elucidating the form of the air-bladder and the modifications undergone

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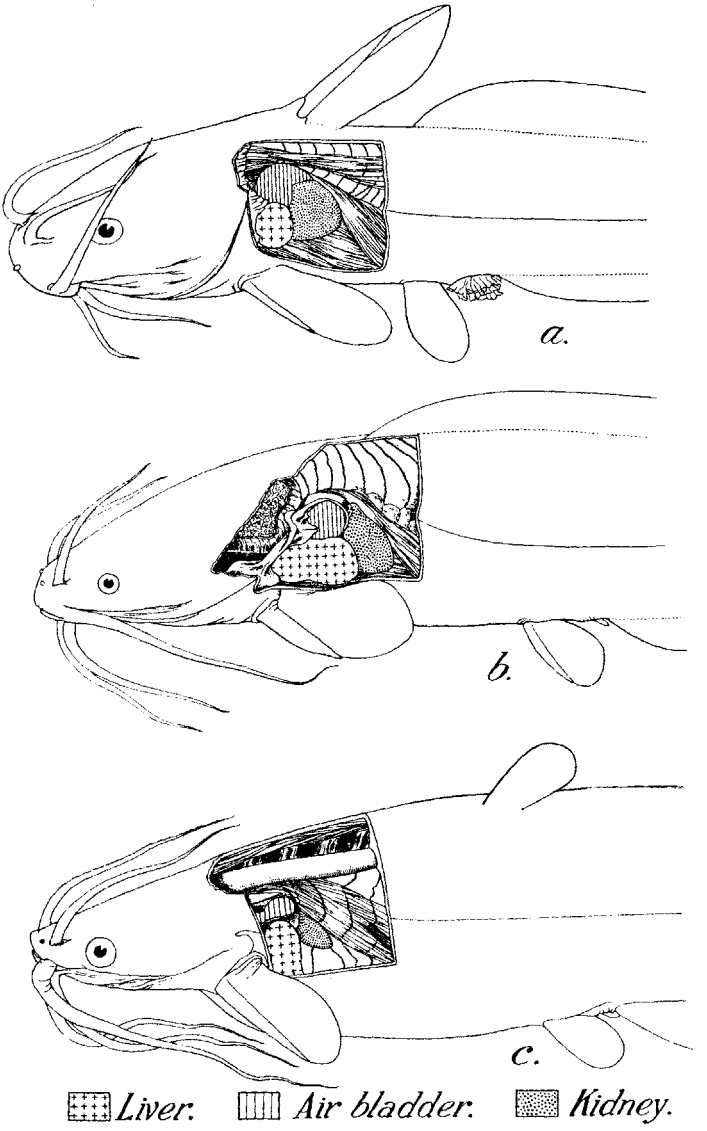


TEXT-FIG. 1.—Dorso-lateral view of the head and anterior part of the body of *Plotosus canius* Ham., *Clarias batrachus* (Linn.) and *Heteropneustes fossilis* (Bloch).

Skin in the region above the pectoral fin is removed to show the disposition of the liver, the air-bladder and the kidneys.

a. Plotosus canius Ham. × 1½; *b. Clarias batrachus* (Linn.). × ¾; *c. Heteropneustes fossilis* (Bloch). Nat. Size.

by the associated skeletal structures. The disposition of the liver and the kidneys was also noted in each case, and it soon became apparent that the

chief factor that had brought about the peculiar disposition of the liver and the kidney in *Clarias*, *Heteropneustes*, etc. was undoubtedly the reduction of the body-cavity, while the actual formation of the extra-coelomic lobes appears to be due to the changes in shape and position of the air-bladder consequent upon the dorso-ventral flattening of the body.

In this note I trace the changes undergone by the air-bladder, the liver and the kidneys from the simple to the most highly specialized forms. As a result of the study of these types there seems little doubt that the remarkable modifications of the air-bladder, as elucidated by Bridge and Haddon in *Ailia* Gray, *Clupisoma* Swainson (=*Schilbeichthys* Bleeker), *Silonia* Swainson (= *Silundia* Cuv. & Val.), etc. are the direct result of the disposition of the liver and the kidneys and are not due to any special physiological requirements of the various forms.

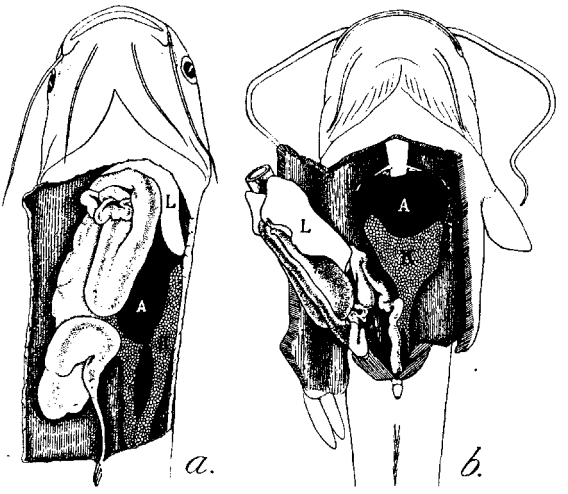
For the purpose of this enquiry Günther's (1864) divisions of the Siluroid fishes into Siluridæ Homalopteræ, Siluridæ Heteropteræ, Siluridæ Proteropteræ, and Siluridæ Proteropodes are of special significance, as they are based on the external extent of the dorsal and the anal fins ; with these is also correlated the relative restriction in the size of the abdominal cavity in the various divisions. As the Siluridæ Proteropodes resemble the Siluridæ Proteropteræ in the form and extent of the anal fin, it will be sufficient to consider here the members of the first three groups only.

Among teleostean fishes, as a rule, the kidneys extend along the entire length of the dorsal wall of the abdomen, above the air-bladder : those of the two sides are partly fused with one another in the middle line. The anterior portion of each kidney is greatly dilated and, in the adult, consists of lymphatic or adenoid tissue only ; as a result, while resembling the rest of the organ in external appearance, it cannot discharge any renal function. This persistent and usually bilobed ' head-kidney ' occupies a recess of a corresponding shape lying in front of the anterior wall of the air-bladder. The liver, whose form is always closely adapted to that of the surrounding parts, lies to a greater or less extent beneath the intestinal tract.

The abdominal region in almost all Siluroid fishes is relatively short, the air-bladder extends at the sides and forms lateral cutaneous areas above the pectoral fins, the kidney is displaced from its normal position and caps the posterior part of the air-bladder, and the lateral lobes of the liver, which are displaced from their normal position, lie in peritoneal cul-de-sacs situated anterior to the lateral extension of the air-bladder.

With the forward extension of the anal fin, the body-cavity becomes still further reduced and as a result two organs, the kidney and the liver, encroach on the space usually occupied by the air-bladder. As a generalized example of the Siluridæ Heteropteræ we may consider the case of the genus *Pangasius* Bleeker which possesses a comparatively short anal fin. In very young specimens of *Pangasius pangasius* (Ham.), below 50 mm. in length, the air-bladder is extensive and its posterior portion in the form of a small hollow

knob-like protuberance lies embedded in the tissues of the kidneys ; this part of the air-bladder represents the portion of the structure that has been squeezed from all sides to provide more space for the kidney. With the growth of the fish the knob-like structure develops into a tubular cæcum and in the adult the air-bladder consists of an anterior large, oval chamber in which the length is greater than the breadth and a posterior long cæcum, constricted in one or more places, extending to the base of the caudal fin.[1] The portion of the cæcum in the abdominal cavity, or in the earlier stages the whole of it, is



TEXT-FIG. 2.—Dissection of the visceral organs of *Pangasius pangasius* (Ham.) and *Silurus cochinchinensis* Cuv. & Val., to show the disposition of the liver (L), the kidneys (K) and the air-bladder (A).

a. Pangasius pangasius (Ham.) × ¾ ; *b. Silurus cochinchinensis* Cuv. & Val. Nat. Size.

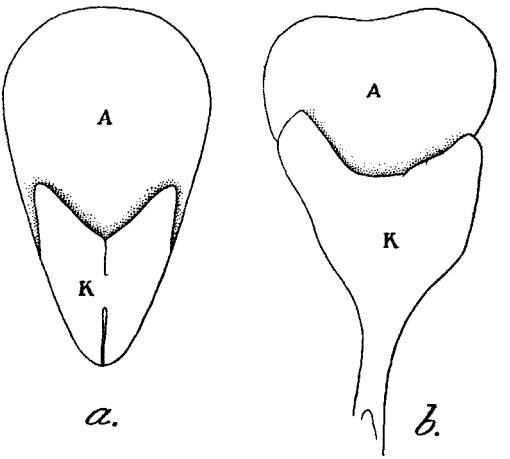
surrounded by the kidneys which also extend laterally at the sides of the anterior chamber. This condition has no doubt resulted from the fact that as the kidneys assumed their normal dimensions they pressed on the air-bladder for more and more space and towards maturity the pressure on the bladder seems to have been so great that a portion of it actually penetrated the muscles of the caudal region to ease the pressure for space in the abdominal cavity. Indian genera of the Siluridæ Heteropteræ may be grouped into three families—Schilbeidæ comprising *Pangasius, Pseudeutropius* Bleeker, *Silonia, Clupisoma, Eutropiichthys* Bleeker and *Ailia* ; Siluridæ comprising *Wallago* Bleeker, *Callichrous* Ham., and *Silurus* Linn., and Heteropneustidæ[2] containing

[1] This also happens in certain species of the genus *Cryptopterus* Bleeker (Family Siluridæ).

[2] Regan (1911) included this in the family Clariidæ, but I (1936 *a*) have given reasons elsewhere that this genus is closely related to the Siluridæ and on account of its special features should be regarded as the type of a distinct family.

Heteropneustes. The last two families and the Siluridæ Homalopteræ are considered first.

According to the general body-form, the Siluridæ may be divided into two sections, (i) in which the body is greatly compressed, such as *Wallago* and *Callichrous*, and (ii) in which the trunk region is at least moderately depressed, such as *Silurus*. In the first two genera the air-bladder is co-extensive with the abdominal cavity ; it is deeper than broad and the lateral walls of its anterior part lie just beneath the skin. The kidneys cap a consider-

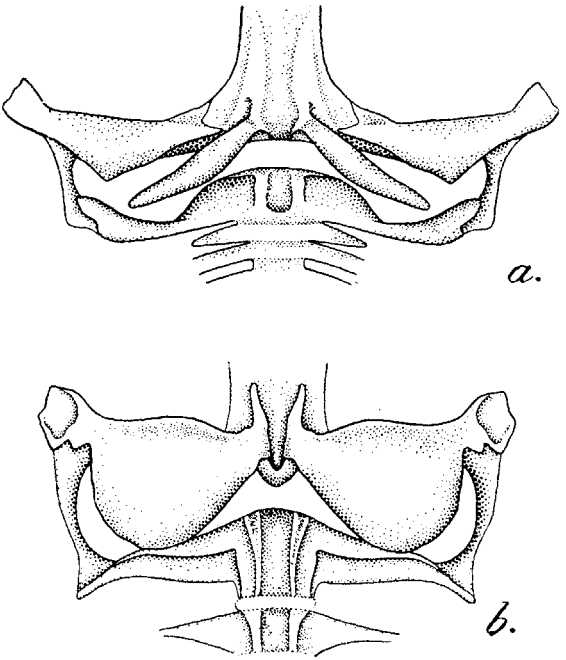


TEXT-FIG. 3.—Air-bladder (A) and Kidneys (K) of *Wallago attu* (Bloch) and *Silurus cochinchinensis* Cuv. & Val.

a. *Wallago attu* (Bloch). × 1⅔ ; *b*. *Silurus cochinchinensis* Cuv. & Val. × 2⅔.

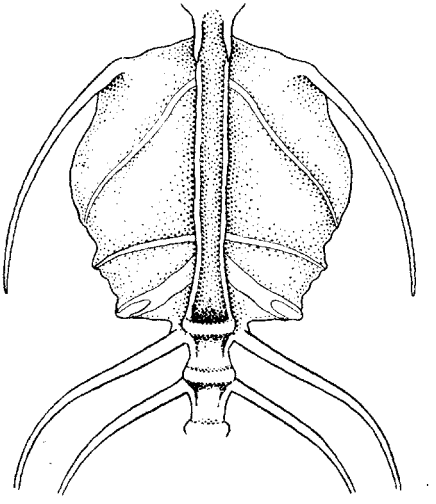
able part of its posterior portion. In *Silurus*, however, the air-bladder occupies only one-third of the length of the abdominal cavity and is broader than long. It is thick-walled, thereby showing that its utility is partly lost. The kidneys are fairly extensive and are broadened anteriorly into a cup-shaped structure in which is lodged the posterior part of the bladder. The liver (text-fig. 2 *b*) is also very extensive, especially on the left side, and lies closely pressed against the air-bladder. In *Olyra* McClelland, an aberrant genus for which I (1936) have proposed a separate family, the air-bladder, though very similar to that of *Silurus*, is still further reduced. The disposition of the liver and the kidneys is very similar to that of *Silurus*, except that the kidneys now extend almost to the areas of the skin beneath which lie the lateral walls of the air-bladder.

If a *Silurus*-like fish were to become greatly depressed, the space inside its body-cavity will be correspondingly reduced, and the forward push of the kidneys would result in the air-bladder assuming a transverse, tubular form, while to combat the forward thrust of these organs the bony elements would be developed in front of the air-bladder. Even in *Olyra* the beginnings of a



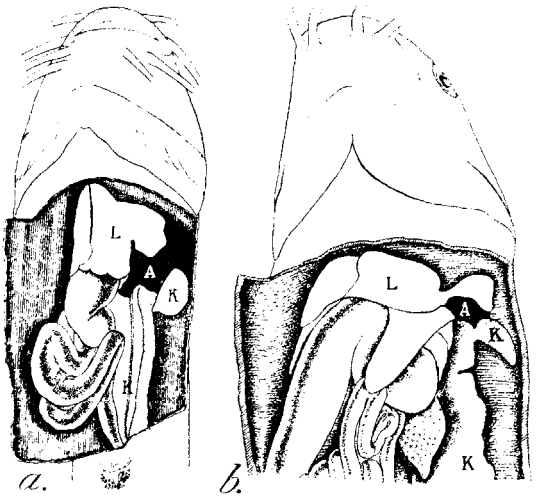
TEXT-FIG. 4.—Air-bladder (unshaded portion) and associated skeletal structures in *Clarias batrachus* (Linn.) and *Heteropneustes fossilis* (Bloch).
a. Clarias batrachus (Linn.). × 4 ; *b. Heteropneustes fossilis* (Bloch). × 4.

protective bony capsule are to be seen in the wing-like expansions of the transverse processes of the complex vertebra which partly envelop the anterior



TEXT-FIG. 5.—Wing-like expansions of the transverse processes of the complex vertebra in *Olyra longicaudata* McClelland. × 7.

part of the bladder. In the hypothetical case taken above, the forward growth of the kidneys, however, would be checked by the air-bladder and its bony capsules. The liver would also be able to extend laterally along with the bladder and come to lie ventral to it, beneath the skin in small extra-coelomic cul-de-sacs. Owing to the space required for the liver, anterior to the bony elements, the 'head-kidneys' would also be displaced from their normal position and pushed outwards round the posterior part of the air-bladder. Such series of changes have, in my opinion, brought about the peculiar dis-



TEXT-FIG. 6.—Dissection of the visceral organs of *Plotosus canius* Ham. and *Heteropneustes fossilis* (Bloch), to show the disposition of the liver (L), the air-bladder (A) and the kidneys (K).

a. Plotosus canius Ham. × ¾ ; *b. Heteropneustes fossilis* (Bloch). × 1¼.

position of the liver and the kidneys in *Heteropneustes* (text-fig. 1 *c*).

It is clear from the above that with the reduction of the body-cavity the kidneys encroach upon the space normally occupied by the air-bladder and thus set up a series of changes which result ultimately in the extrusion of small lobes of the liver and the kidneys into extra-coelomic spaces. With regard to the displacement of the liver, Bridge and Haddon have already noted (1893, p. 226) that

'In nearly all Siluroids the lateral growth of the air-bladder, and the intimate relation of its outer walls to the lateral cutaneous areas, have led to the displacement of the lateral lobes of the liver and their enclosure within peritoneal cul-de-sacs, a condition which sometimes persists even in cases where the air-bladder has undergone partial atrophy.'

Dutta (1924) showed that the extra-coelomic kidney in *Clarias* and *Heteropneustes* is devoid of any uriniferous tubules, Malpighian capsules and glomeruli and concluded that these facts 'definitely and clearly indicate that this portion of the kidney is a non-functional and degenerate organ'. Evidently he appears to have overlooked the fact already referred to above (*supra*,

p. 33) that in all teleostean fishes the anterior end of the kidney is usually converted into adenoid or lymphatic tissue, and though resembling the rest of the organ, it does not discharge a renal function. It has also been noted above that the ' head-kidney ' only is pushed outwards into the extra-coelomic sacs. The modified lymphatic tissue of the ' head-kidney ' probably discharges some very vital functions, as in spite of the lack of space for the extension of the kidney proper, it is being retained as a fairly large structure. In this connection it is very significant to note that the extra-coelomic portion of the liver has probably undergone no degeneration, as it was found by Dutta to be histologically exactly similar to the normal portion of the liver inside the body-cavity.

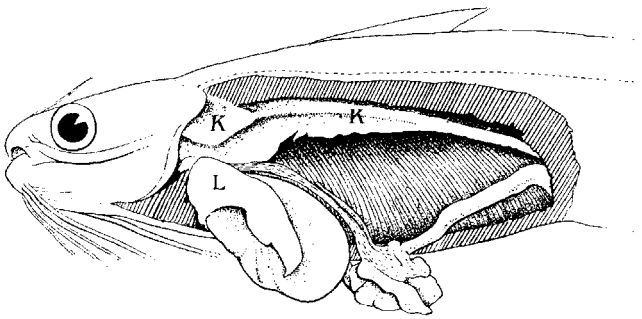
The Siluridæ Homalopteræ may next be considered. These forms, besides showing an antero-posterior reduction of the body-cavity, are characterized by the greatly depressed form of the body, similar to that of *Heteropneustes*. The three Indian genera of this division—*Chaca* Gray, *Plotosus* and *Clarias*, are now regarded as belonging to three different families which probably have no genetic affinity with one another. *Chaca*, with a greatly depressed form, has a relatively much more spacious body-cavity ; the disposition of the air-bladder, the liver and the kidneys in this genus is similar to that of *Silurus*. In *Plotosus* (text-fig. 1 *a*) the bladder is considerably reduced, is broader than long and its lateral walls lie beneath the skin. As usual the kidneys cap its posterior portion, while lobes of the kidneys (presumably the ' head-kidneys ') extend laterally along the bladder and come to lie beneath the skin. The liver also caps the anterior part of the bladder and sends out broad lateral flaps, which in younger specimens come to lie beneath the skin. In *Clarias* (text-fig. 1 *b*) the disposition of the liver, the kidneys and the air-bladder is very similar to that described above for *Heteropneustes*. As in the latter genus the air-bladder of *Clarias* also is in the form of a fairly wide, horizontal tube which is partially enclosed in bone (text-fig. 4 *a*).

So far I have considered the modifications undergone by the air-bladder, the kidneys and the liver consequent upon the reduction of the abdominal cavity both antero-posteriorly as well as vertically. During these changes the organs could only extend laterally into the muscles of the anterior region of the body wall. In the Schilbeidæ the reduction of the body-cavity is effected through the compression of the body, resulting in the specialized genera of the family assuming a Clupeid form in which the body is greatly compressed and the ventral surface almost forms a sharp keel. *Pangasius*, to which a reference has been made above (*supra*, p. 3), is, in my opinion, a generalized representative of the family Schilbeidæ, so we may start our series with that genus. In the course of evolution this genus, as I have shown elsewhere,[1] gave rise to

[1] In my revision of the Indian Schilbeidæ to be published in the *Records of the Indian Museum* for 1937 I have discussed the systematic position of *Pangasius* and shown the evolution of most of the other genera from this generalized type.

very diverse forms. Some of these are discussed below. In *Pseudeutropius*, as also in *Eutropius* Müll. & Trosch., *Schilbe* Cuv. and *Silurandon* Bleeker of Africa, the air-bladder is fairly extensive, in some forms it is co-extensive with the abdominal cavity while in others it is of the same nature as in *Silurus*, *Olyra*, etc., and the disposition of the liver and the kidney is also similar to that of either *Wallago* or *Silurus* (*vide supra*, p. 35). In certain species the lateral walls of the anterior portion of the bladder come to lie just beneath the skin and are to be distinguished externally as translucent, blister-like areas above the pectoral fins ; while in other forms the bladder is fairly thick-walled and occupies only one-quarter to one-half the length of the body-cavity.

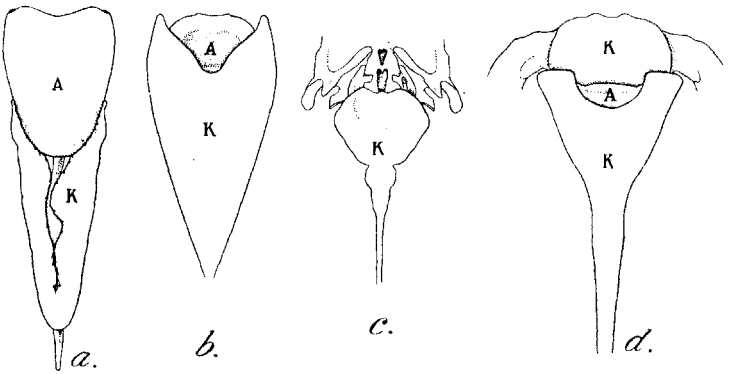
As the body-cavity became more and more reduced antero-posteriorly, as also laterally, important adjustments occurred in the disposition of the air-bladder, the kidneys and the liver. In *Clupisoma*, for instance, the normal kidneys not only pushed the air-bladder forwards but are also extended over its ventral surface. The ' head-kidneys ', which were displaced from their normal



TEXT-FIG. 7.—Dissection of the visceral organs of *Clupisoma garua* (Ham.), to show the disposition of the liver (L) and the kidneys (K). × 1⅓.

position, form lateral lobes at the sides of the kidneys within the coelomic cavity. Further, owing to the great reduction of the body-cavity in its ventral portion the liver was displaced into the dorsal portion of the cavity, and presses the air-bladder from below. Under these circumstances the air-bladder of *Clupisoma* became greatly reduced and flattened. In some other genera, however, such as *Silonia*, *Eutropiichthys* and *Ailia*, the liver appears to have exerted more pressure on the air-bladder from below and the normal kidneys pushed it from behind so that it became greatly reduced and its central area became more or less solid or disappeared altogether. In young specimens of *Silonia* the air-bladder consists of a small, rounded structure with the normal kidneys capping its posterior part and the liver making a fairly broad depression in its middle. With the growth of the fish the kidneys extend forwards and the liver impinges on the air-bladder from below with the result that the bladder ultimately becomes divided into two portions, slightly united anteriorly, which come to lie in deep recesses formed in the transverse processes of the

complex vertebrae. The 'head-kidneys' are in their normal position anterior to the air-bladder. In *Eutropiichthys* the air-bladder is tubular and horse-shoe-shaped, but its posterior part is covered by the kidneys which provide a wide depression on the ventral surface for the liver. Even here the 'head-kidneys' are in their normal position. In *Ailia*, the most highly compressed fish among the Indian Schilbeidæ, the tubular, and horse-shoe-shaped air-bladder is covered anteriorly by the 'head-kidneys' and posteriorly by the normal kidneys which extend on the sides and occupy a considerable area in front of the posterior boundary of the air-bladder. Only a small portion of the air-bladder, however, is seen between the kidneys. The anterior part of the air-bladder is covered by a bony structure which now separates the 'head-



TEXT-FIG. 8.—Disposition of the kidneys (K) and the air-bladder (A) in certain Indian genera of the Schilbeidæ.

a. Pangasius pangasius (Ham.), half-grown specimen with a portion of the air-bladder extending into the caudal region. × ⅔; *b. Silonia silundia* (Ham.), young specimen, 135 mm. in total length. × 1¾; *c. Eutropiichthys vacha* (Ham.), young specimen, 140 mm. in total length. × 1¼; *d. Ailia coila* (Ham.), half-grown specimen, 88 mm. in total length. × 3¼.

kidneys' from the vital part of the bladder itself. Though *Ailia* and *Eutropiichthys* are probably not very closely related forms, the similarity in the structure of their air-bladder appears to have been induced by similar circumstances.

Reference may here be made to an extra-Indian form, the Siamese genus *Platytropius* Hora,[1] as it exhibits remarkable modifications. I have shown that its air-bladder is greatly flattened dorso-ventrally and has assumed a more or less leaf-like form.[2] The kidneys in this case lie in their normal position dorsal to the air-bladder but are greatly flattened. The 'head-kidneys' are situated in their normal position.

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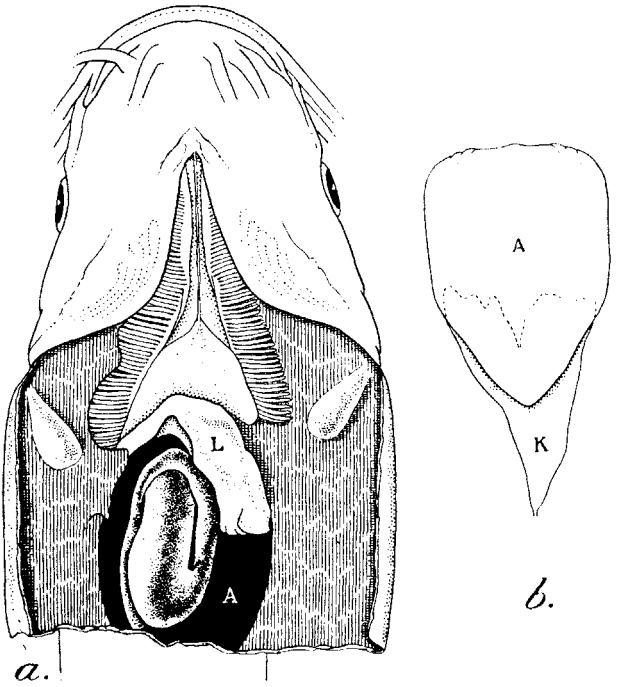
[1] Genotype: *Pseudeutropius siamensis* Sauvage. This new genus will shortly be described in the *Journal of the Siam Society*, Natural History Supplement.

[2] In *Osteogeniosus*, in which the air-bladder is more or less of the same type as that of *Platytropius*, the disposition of both types of kidneys is also similar.

From the modifications detailed above it is clear that for the peculiar disposition of the liver and the kidneys the initiative is provided by the forward extension of the caudal region and the consequent reduction of the space in the body-cavity. The necessary adjustments for the accommodation of the various organs in the reduced space are effected in various ways, mainly depending on the form of the body-cavity. In dorso-ventrally flattened forms there is a lateral extension of the organs, and the lateral portions of the air-bladder, the liver and the kidneys all come to lie just beneath the skin,



TEXT-FIG. 9.—*Platytropius siamensis* (Sauvage).

a. Dissection of the visceral organs to show the disposition of the liver (L) and the air-bladder (A). × 1½; *b*. Disposition of the air-bladder (A) and the kidneys (K). × 5¼. Dotted line represents the extent of the kidneys dorsal to the air-bladder or the portion of the kidneys covered by the air-bladder on the ventral surface.

as in *Plotosus*, *Clarias*, *Heteropneustes*, etc. If, on the other hand, the body is compressed from side to side the kidneys may lie in their normal position under a very much flattened air-bladder as in *Platytropius*, or may gradually push the air-bladder forwards till the latter, unable to expand laterally, becomes reduced to form a narrow horse-shoe-shaped tube, as in certain genera of the Schilbeidæ. I am of opinion that no special physiological value can be attached to these anatomical features which are obviously the result of a morphological adjustment consequent upon the reduction of the abdominal cavity. The air-bladder does not appear to be an organ of primary importance in the economy

of life of these fishes, and whenever more space is required, either for the liver or the kidneys, nature provides it at the expense of the air-bladder.

Summary.

The present views with regard to the peculiar disposition of the liver and the kidney are given and it is indicated that though no satisfactory solution of the problem has yet been suggested, the shortening of the body-cavity has been assumed to be the main cause both by Bridge and Haddon and Dutta, whereas Weber attributed the peculiarities to the lateral expansion of the air-bladder.

Günther's system of classification of the Siluroid fishes has been followed in this article as a matter of convenience. Generally in the Siluroid fishes the body-cavity is small and the liver and the kidneys are somewhat displaced from their normal position. In Siluridæ Heteropteræ, in which the dorsal fin is short and the anal fin long, the changes in the form and disposition of the air-bladder, the liver and the kidneys are dealt with in a progressive series from a primitive form like *Pangasius* to such highly specialized genera as *Clupisoma*, *Eutropiichthys* and *Ailia* of the Schilbeidæ and *Heteropneustes* of the Heteropneustidæ. The changes due to compression and depression of the body are shown to be of a very different nature; in the Schilbeidæ, in which the body is compressed, the air-bladder becomes greatly reduced and in extreme cases forms a horse-shoe-shaped tube, the functional kidneys may, wholly or partly, extend over the reduced air-bladder, while the liver is pushed upwards and presses on the air-bladder. In Heteropneustidæ, in which the body is depressed, the air-bladder assumes the form of a fairly wide transverse tube which extends laterally to the skin; along with the air-bladder, the liver and the kidneys also extend laterally and come to lie beneath the skin on the two sides of the air-bladder. In the three Indian genera of the Siluridæ Homalopteræ, *Chaca*, *Plotosus* and *Clarias*, the body is greatly depressed; their air-bladder, kidneys and liver show a series of changes leading to the condition described in the Heteropneustidæ. Reference is also made to the modifications observed in *Platytropius*, a Siamese genus.

It is concluded that the main cause of these modifications is the shortening of the body-cavity and the subsequent adjustment of the organs within the short space available.

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