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THE SCALES OF THE AFRICAN
CHARACINID FISHES

WITH TWO PLATES

BY

T. D. A. COCKERELL

University of Colorado, Boulder, Colo.



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THE SCALES OF THE AFRICAN CHARACINID FISHES

By T. D. A. COCKERELL

UNIVERSITY OF COLORADO, BOULDER, COLO.

(WITH TWO PLATES)

As primitive relatives of the Cyprinidæ, confined to the Neotropical and Ethiopian regions, the Characinidæ (or Characidæ) are of more than usual interest to students of the evolution of fishes. After having spent much time in the investigation of the scales of the Cyprinids, I was very anxious to see those of the Characinids, and the opportunity was offered during a recent visit to the British Museum. For all the material used in the preparation of the present paper I am indebted to the kindness of Dr. G. A. Boulenger, who has in his custody at the British Museum a truly wonderful collection of African freshwater fishes, as every ichthyologist knows. It was an extraordinary privilege to have access to these rich materials, which had been gathered with so much difficulty and sometimes danger, and had formed the basis of classical researches.

The sculpture of an ordinary fish-scale includes two important elements, the circuli and the radii. The circuli are circular lines, sometimes referred to as "lines of growth," while the radii are lines or grooves radiating outward from the nuclear area, which may or may not be in the center of the scale, but is practically always in the middle line. The most primitive fish with scales resembling those of the Teleosts is *Amia calva*, and through the kindness of Dr. B. W. Evermann I have been able to examine specimens of this fish from the Yellow River at Plymouth, Indiana. There are no radii, but the scales are made up of longitudinal strands which are really separable elements, and will fray out basally. These appear on the scale as very fine striæ which in the apical field are directed toward a broad rugulose nuclear area. There is no doubt, I think, that these are the circuli of the Teleosts, and indeed they are nearly repeated in various forms, though I know no scale which as a whole can be said to closely resemble that of *Amia*.¹ This view

¹ I placed a scale of *Polypterus endlicheri* (from the White Nile) in acid to ascertain the structure of the organic basis, which proved to be rather scanty and of a sponge-like consistency.

suggests the probability that the Teleosts with very fine and dense circuli (*e. g.*, the majority of the Old World Cyprinids) are so far more primitive than those in which the circuli are fewer (*e. g.*, the New World Cyprinids, but *not* the Catostomids), as had already been assumed on other grounds.

The radii, according to this theory, are of secondary origin. In some cases they may lose their radial arrangement, and more or less simulate circuli. This is seen in *Alosa sapidissima* Wilson (fig. 1), the circuli of which are extremely fine and delicate, while the radii of the basal field actually take the form of widely spaced transverse,

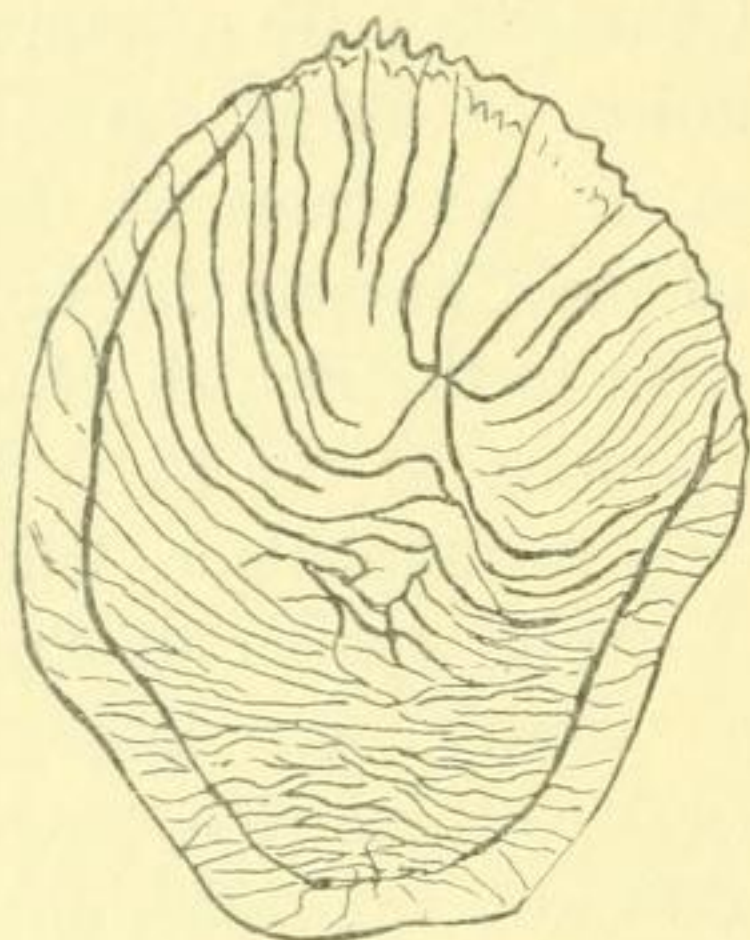


FIG. 1. *Alosa sapidissima*
Wilson

Drawn by Miss E. V. Moore

almost concentric lines. In some of the scales (the larger and broader ones) this development is so complete as to conceal its origin, but in other scales on the same fish the various transitional states can be perceived.

On the other hand the circuli may also become transverse, losing the appearance of concentric lines. This is excellently shown in *Scomber chrysozonus*, from Massauah (pl. 1, fig. 1); that the lines really are circuli is proved by the scale of *Scomber pneumatophorus* (Table Bay, Cape of Good Hope), (pl. 1, fig. 2), in

which they are still obviously circuli.

The African Characinidæ have scales of two main types, which seem to be wholly distinct. The first, including the Hydrocyoninæ and Citharininæ, may be called the Cyprinoid type, showing a distinct—often strong—resemblance to the scales of the Cyprinidæ. In this type the nuclear area is central, or nearly so, and the scales are usually cycloid, rarely ctenoid, and when so not at all like the ctenoid scales of the other group.

The second or ctenoid group proper includes the Ichthyoborinæ and Distichodontinæ, which cannot be separated on the squamation. In this series the apical teeth are very regular and numerous, united laterally, and the nuclear area is almost at the apex, the base being thrown more or less into folds. This basal folding appears to lead to the very distinctive system of basal radii found in the Acanthopterygian and allied fishes; *e. g.*, in *Tilapia nilotica* (Cichlidæ), (pl. 1, fig. 3), *Apomotis cyanellus* (Centrarchidæ), *Cyprinodon fasciatus* (Cyprinodontidæ), and *Anabas munii* (Anabantidæ).

This type of basal radii thus runs through the Haplomi, Acanthopterygii and Percesoces; yet it is wholly absent in the Scombrids, so far as I know, and *Gadus* (cf. H. W. Marett Tims, Quart. Journ. Micr. Science, Oct., 1905) shows nothing of it. (The scale of *Gadus* is curiously like that of *Catostomus*.) The ctenoid features found in *Anabas* seem to be traceable to a Berycid source. It is evident, of course, that no Acanthopterygian fish can be derived from any Characinid stock, but it is suggested that the basal folding was developed among the Malacopterygians (*Alosa* shows it sufficiently well) and carried thence to the Characinid and Acanthopterygian (or Haplomid) ancestors.

I hope in some later contribution to compare the South American Characinid scales with the African. At present I cannot do this for lack of material, but the little I know suggests that there may be little resemblance between them.

(Figure 2 (drawn by Miss Evelyn V. Moore) shows the scale of *Cheirodon insignis* Steindachner from Panama; this fish is placed by Boulenger in the Hydrocyoninae, but it will be seen that there is no resemblance to the scales of any of the African members of that subfamily. The scale of *Luciocharax* is quite unlike anything African, but this belongs to an exclusively American subfamily (Xiphostominae).

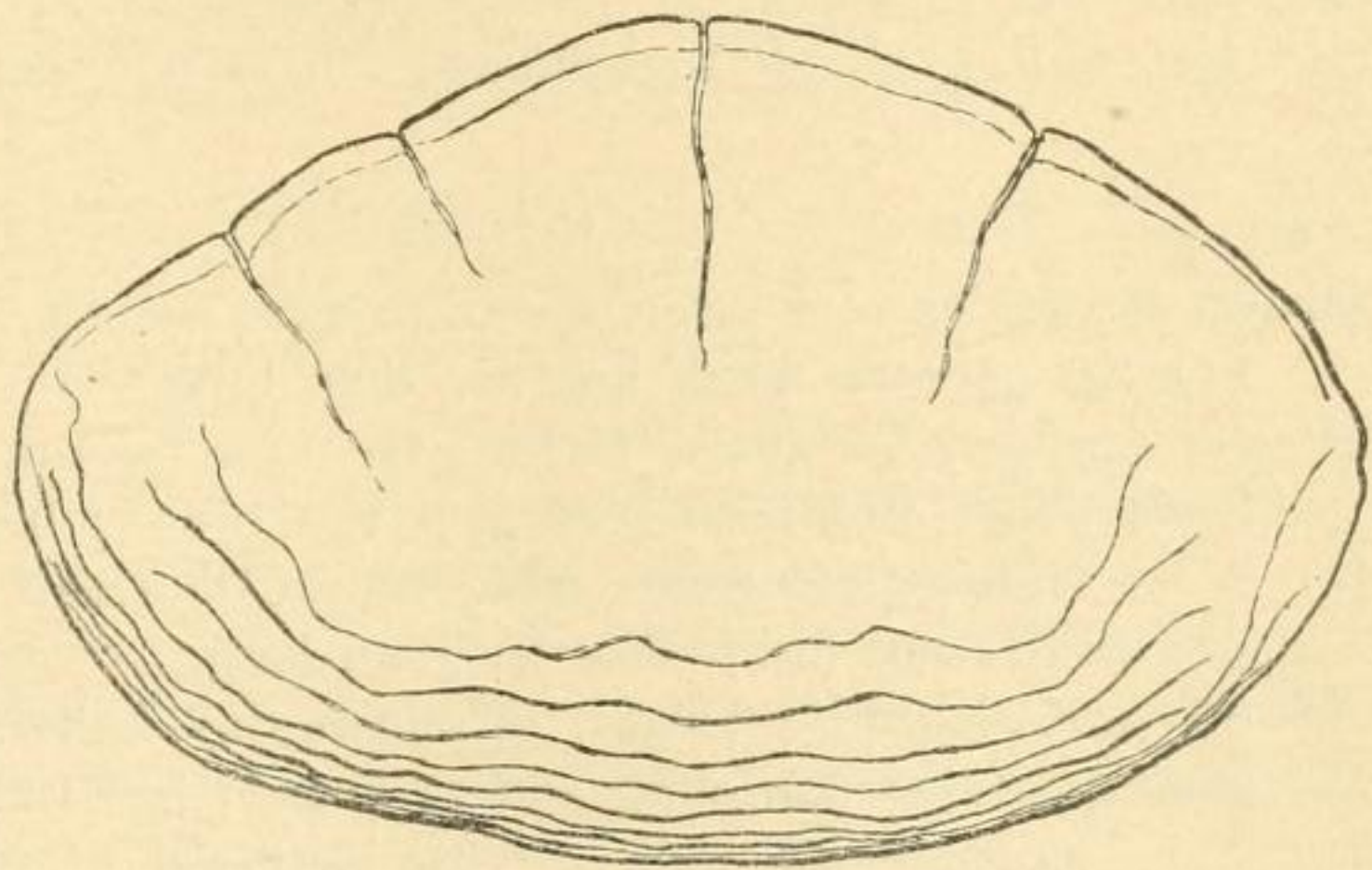


FIG. 2. *Cheirodon insignis* Steindachner

For the means of obtaining the photographic figures (the work of Mr. T. C. Black, of Boulder, Colorado) I am indebted to a grant from the American Association for the Advancement of Science. It may be worth while to state that in order to get good photographs the scales must be mounted dry. When placed in balsam many of the characters are obscured.

HYDROCYONINÆ

The scales of the African Hydrocyoninae fall naturally into three groups:
 (1) *Sarcodaces* group, in which the approximately circular scales have fine and rather numerous radii, and the circular sculpture is very distinct, the apical circuli very coarse and quite different from the basal and lateral. *S. odoë* examined.

- (2) *Alestes* group, including *Alestes*, *Micralestes*, and *Petersius*, in which the radii are few but very strong, the sculpture is often weak in the apical region, and the scales are frequently much broader than long.
- (3) *Hydrocyon* group, in which the apical field is more or less rugose, and the radii are evanescent, the basal radii usually absent. The dorsal scales of *Hydrocyon* show numerous but very weak apical radii, which produce some crenulation of the very thin margin, indicating a slight approach to a ctenoid condition. *H. forskalii* examined.

It appears probable that *Sarcodaces odoë* (River Benue, north of Ibi, *H. L. N. Traill*) has the more primitive type of scale. *Hydrocyon forskalii* (River Nile) can be derived from this by the general weakening of all the structures; while the *Alestes* group represents a reduction of the radial system, with a much stronger development of what remains. Thus three fairly distinct tribes would appear to be indicated: Sarcodacini, Alestini, and Hydrocyonini, their typical genera *Sarcodaces*, *Alestes*, and *Hydrocyon* respectively. The term Hydrocyonini was used by Bonaparte as early as 1838 (*Nuovi Annali delle Sci. Nat.* 2, p. 132). *Bryconæthiops* I have not seen.

ALESTES

Group A. Scales very large, the transverse diameter over 15 mm.

- (1) Scales very much broader than long.

Alestes tæniurus Günther. Kribi River, Cameroon (*G. L. Bates*).

Scale about 10.5 mm. long and 16.5 broad; basal radii about 12; discal region divided into many polygonal areas.

- (2) Scales not much broader than long.

Alestes rhodopleura Boulenger. Mtondwe Bay, Lake Tanganyika (*Cunnington*).

Scale about 18 mm. long and 21 broad; basal radii two; lateral radii two on each side, more or less inclined to be divided or delta-like marginally; apical radii few and quite irregular; apical region rugose; circuli of basal region extremely fine.

Alestes macrolepidotus Cuvier and Valenciennes. River Nile. Structure essentially as in *A. rhodopleura*; rugosity of apical region, resulting from modified circuli, very pronounced. The discal region may be reticulate.

Group B. Scales smaller, the transverse diameter much less than 15 mm.

Owing to individual variation and the small amount of material available it is impossible to determine the precise specific characters in this group. Some of the species probably cannot be separated on the scales. In no case are the scales of the very broad *tæniurus* type.

- (1) Comparatively large reddish scales, with the apical rugosity poorly developed.

Alestes macrophthalmus Günther. Lake Tanganyika (*J. E. S. Moore*).

Radii very few and feeble, in the single scale examined there is only one basal; scale about 7.5 mm. long and 9 broad.

Alestes liebrechtsii Boulenger. Coquilhatville, Upper Congo (*Delhez*).

Radii more numerous, about six basal, but two of these incomplete; discal region with some polygonal areas; scale about 8.5 mm. long and 10.5 broad. The characters separating these two are doubtless variable.

- (2) Rather large white scales, with the apical circuli forming conspicuous strong ridges; the basal circuli, as usual, very fine.

Alestes affinis Günther. Wabbi System (*O. Neumann*).

Only one basal radius; apical region with the radii branching and anastomosing quite irregularly, all very strong; scale about 7 mm. long and 8 broad.

Alestes imberi Peters. Lake Nyassa (*Capt. E. L. Rhoades*).

Thinner scales than those of *A. affinis*; basal radii three; apical region quite as in *A. affinis*. Scale about as broad as long.

- (3) Rather small (6 to 7 mm. diameter) whitish scales of a rather broad type, having the outline of a little more than a half circle; apical sculpture feeble; basal radii three or four. There is no sign of the apical structure described under *A. affinis*. These scales are certainly nearer to the *macrophthalmus* group than to the *affinis* group.

Alestes (Brachyalestes) longipinnis Steindachner. Sette Cama, Gaboon (*Gerrard*).

Alestes chaperi Sauvage. Kotchwah River (*R. B. N. Walker*).

These two were united by Günther, and certainly there is no difference in the scales.

- (4) Small scales about 6 mm. diameter or less, without very marked characters.

Alestes sadleri Boulenger. Entebbe, Lake Victoria (*Degen*).

Polygonal areas present or absent; apical circuli rather strong.

Alestes lateralis Boulenger. Kafue River, Upper Zambesi (*T. Codrington*).

Scale small, but not from a fully-grown fish. Only one basal radius.

Alestes intermedius Boulenger. Kribi River, Cameroon (*G. L. Bates*).

Scale rather broad, with five basal radii; apical sculpture very feeble; lateral circuli, especially in the subdiscal region, much less dense than usual, and minutely wavy or zigzag.

Alestes nurse Rüppel. River Nile.

Basal radii variable up to about six; polygonal areas present or absent.

Alestes baremose Joannis. River Nile.

Basal radii one or two; polygonal areas not observed; scale in general similar to that of *A. nurse*, but differing in important details, as shown below.

The scales described above were all taken from the vicinity of the lateral line, about the level of the beginning of the dorsal fin. The following notes describe the variation observed on the different parts of the fish.

Alestes macrolepidotus. This species is remarkable for the very large scales, and the posterior situation of the first dorsal fin. The borders of the scales are beautifully purplish-iridescent, but the fish is not silvery like *A. nurse* and *baremose*. The coarse apical circuli become entirely longitudinal, suggesting the corresponding structures in *Amia calva*, in which the progenitors of the circuli are longitudinal strands. The apical radii largely anastomose transversely, resulting in the formation of very irregular transverse markings, few in number. In the ventral region the sculpture is more profuse, and the apical field develops a sort of cancellation, in which the *longitudinal* lines appear to represent modified circuli, and the *transverse* modified radii. The anterior dorsal scales are again quite different, with

a curiously *Amia*-like sculpture, composed almost altogether of elements representing the circuli, but consisting of coarse longitudinal striæ or strands, which are, however, continuous with the usual extremely fine and regular circuli of the concealed portion of the scales, the latter having about three strong basal radii and one on each side.

Alestes nurse. Very similar in appearance to *A. baremose*, but deeper-bodied. The strong apical circuli are mainly longitudinal, meeting at an acute angle in the middle line. The apical radii often have transverse branches, more or less in the manner of a spreading tree; usually there is a single apical radius, with branches leaving at right angles, but in the dorsal and ventral regions there are more.

Alestes baremose. The sculpture, on close comparison, is really very distinct from that of *A. nurse*. The apical circuli, instead of forming regular grooves, are evanescent, reduced to a fine rugosity; the apical field is sparsely punctate; the one to three apical radii are usually incomplete, and show no lateral branches. The ventral and dorsal scales show many thin, weak, parallel apical radii.

Alestes opisthotania Boulenger, from Efulen, Cameroon (*G. L. Bates*) has rather large (about 8 mm. long and 10 broad) white scales, resembling those of the *affinis* group; with four basal radii, discal polygonal areas, and coarse apical circuli. The interesting feature of the scale is, however, that it is subctenoid, with small but very evident apical denticulations. The teeth are broader than long, and indicate the beginning of such structures as are found, much better developed and much reduced in number, in *Citharidium ansorgii*. The ctenoid scales of *Distichodus*, *Xenocharax*, etc., are entirely different. There are slight indications of apical denticulation in some other *Alestes*, as *A. rhodopleura* and *A. imberi*.

MICRALESTES

The scales of this genus cannot be distinguished from those of *Alestes*; that is to say, there is no *generic* difference, though *specific* distinctions may be found to separate any particular species of *Micralestes* from any particular *Alestes*. The scales are always conspicuously broader than long.

Group A. Apical circuli strong, coarse, and complete, those of the two sides meeting at an obtuse angle.

Micralestes holargyreus Günther. Boma (*Delhez*).

Scale 3.5 mm. long, 5.33 broad; six radii, all strong and complete, one apical, one basal, and two on each side; no polygonal areas. In *Alestes* it comes near to *A. longipinnis*, but it is a shorter scale, with much better developed apical sculpture.

Group B. Apical sculpture feeble, the circuli ill-defined, although the basal circuli are very distinct.

Micralestes altus Boulenger. Lindi, Congo (*Brussels Museum*).

Scale about 5 mm. long and 7 broad; basal circuli much denser than lateral; three basal radii, one apical, one or two on each side; no polygonal areas. (These characters will vary; I doubt whether there is any constant difference in the radii between the species of *Micralestes*.)

Micralestes humilis Boulenger. Ja River, S. Cameroon (G. L. Bates).

Scale about 4 mm. long and 5.33 broad; structure as in the last. Basal radii one to six; apical one to two; polygonal areas present or absent.

Micralestes interruptus Boulenger. Stanley Pool. Congo Free State.

Scale small, only about 3.33 mm. wide; structure as in the others, but basal circuli less dense. Five basal and three apical radii; polygonal areas present.

None of the *Micralestes* show any branching of the apical radii.

PETERSIUS

The scales of *Petersius* are quite as in *Micralestes*, having the same broad form, with few radii, the apical never branching.

Group A. Scale relatively large, about 6 mm. long and 9 broad; apical sculpture very feeble.

Petersius major Boulenger. Nyong River, Cameroon (G. L. Bates.)

Basal radii four, apical two.

Group B. Scale smaller, diameter about 5 mm. or rather less. Apical circuli better developed.

Petersius occidentalis Günther. Infoan (Walker).

Basal radii about four, variable; sides of scale flatter than in the next.

Petersius hilgendorfi Boulenger. Kutu, Lake Leopold II (Delhez).

The scale examined has only four radii, one basal. Its outline is that of a half circle.

Petersius caudalis Boulenger. Boma (Delhez).

Basal radii two or three; small polygonal areas sometimes developed. The smallest of the *Petersius* scales.

CITHARININÆ

Herbivorous fishes, with the teeth minute or absent. Gill (Proc. U. S. Nat. Mus. 18, p. 207) suggests that this group should perhaps constitute a distinct family, Citharinidæ. The scales are subcircular to transversely oval, *without basal radii*, wherein they differ from the African Hydrocyoninæ, excepting *Hydrocyon*.

The following table separates the scales of the species studied:

Scales ctenoid, with large, sharp apical teeth, but these few and far apart, wholly unlike those of *Distichodus*, etc.; nuclear area nearly central, and with circuli to middle; circuli very strong, only moderately dense; scales about 2.33 mm. long and 3.67 broad..

.. *Citharidium ansorgii* Boulenger,
Lake Oguta, Nigeria (Ansorge).

Scales cycloid	1
1. Apical area with fewer and coarser circuli, abruptly marked off from lateral	2
Apical area not, or not very abruptly, marked off from lateral.....	4

2. Broad scale with very many apical radii; nuclear area granular; scale about 7 mm. long and 10 broad, the largest of the Citharinine scales.....*Citharinus gibbosus* Boulenger. Niamkolo, Lake Tanganyika (*Cunnington*).
Rounder scales, with fewer apical radii; nuclear area with circuli to middle 3
3. Scale larger, nearly 6 mm. long, about 7 broad; character of sculpture entirely as in *C. gibbosus*.....*Citharinus macrolepis* Boulenger. Boma, Lower Congo (*Delhez*).
Scale smaller, about 5 mm. broad; otherwise practically the same..
..*Citharinus latus* Müller and Troschel. Beni Souef (*Loat*).
4. Nuclear area with circuli to middle; apical area with very large, coarse circuli, but not quite abruptly separated from lateral; scales small, a little over 3 mm. wide....*Citharinus citharus* Geoffroy (*geoffroyi* Cuvier). White Nile (lake near) (*Loat*).
Nuclear area broadly granular; apical circuli coarse; scale 4.33 mm. broad..
..*Citharinus congicus* Boulenger. Bolobo, Congo (*Grenfell*).

The above key is not wholly satisfactory, because the scales of *Citharinus* are really of a very uniform type, without very obvious specific characters. Two tribes are indicated: Citharidiini for *Citharidium*, and Citharinini for *Citharinus*.

Boulenger places two American genera in this subfamily, but Gill separates them as Curimatinae. I have not seen their scales.

Hydrocyon forskalii runs in the above table near *Citharinus congicus*, but the resemblance is merely superficial.

ICHTHYOBORINÆ

Carnivorous forms with ctenoid scales. There is nothing to distinguish their scales from those of the Distichodontinae. The apical teeth are numerous and close together, having little in common with those of *Citharidium*. The species examined are:

Phago boulengeri Schilthuis. Monsembe, Upper Congo (*J. H. Weeks*).

The scales are hard, bone-like plates joined together, but the apical densely-set spine-like teeth are quite as in the other forms.

Eugnathichthys eetveldii Boulenger. Monsembe, Upper Congo (*J. H. Weeks*).

Small subquadrate scales, with the nucleus apical, just below the row of teeth; no radii, but the basal region is broadly plicate.

Ichthyoborus besse Joannis. Fashoda (*Loat*).

Scales practically as in the last.

Neoborus ornatus Boulenger. Monsembe, Upper Congo (*J. H. Weeks*).

Scales also as in *Eugnathichthys*, except that the apical region is coarsely rugose.

Paraphago and *Mesoborus* have not been examined.

DISTICHODONTINÆ

Herbivorous (or partly herbivorous) fishes with ctenoid scales, which resemble those of the Ichthyoborini. The fact that *Eugnathichthys* and *Ichthyoborus* have quite similar scales, and the absence of any characteristic difference between the scales of the Ichthyoborine and Distichodontine fishes, show that after the development of this type of squamation differentiation took other directions; hence the scales fail to afford any adequate clue to the minor subdivisions of these groups.

In some *Distichodus* (*notospilus*, *sexfasciatus*, *atroventralis*, *engycephalus*) the subapical (exposed) part of the scale is more or less grooved or subreticulate, but otherwise there are no substantial differences between the genera and species examined, which are as follows:

Nannocharax fasciatus Günther. Kribi River, Cameroon (Bates).

Nannocharax niloticus Joannis. River Nile.

The *Nannocharax* scales are the smallest of the series, less than 2 mm. broad. This accords with the small size of the fishes.

Neolebias unifasciatus Steindachner. Ja River, Cameroon (Bates).

Scales about 2.33 mm. broad.

Nannæthiops uniteniatus Günther. Sette Cama, Gaboon (Gerrard).

Scales about 4 mm. broad; basal plication very strong. The scales are longer in proportion to their breadth than those of *Neolebias*.

Xenocharax spilurus Günther. Ibali, Lake Leopold II (Delhez).

Scales about 4.25 mm. long and 5 broad.

Distichodus antonii Schilthuis. Monsembe, Upper Congo (Weeks).

In this species and *D. atroventralis* the scale is unusually broad in proportion to its length.

Distichodus atroventralis Boulenger. Kutu, Lake Leopold II (Delhez).

I do not know how to distinguish the scale definitely from that of *D. antonii*.

Distichodus engycephalus Günther. River Nile at Cairo (Loat).

Scales not quite 5 mm. long, about 6 broad; apical (exposed) area reticulate.

Distichodus fasciolatus Boulenger. Monsembe, Upper Congo (Weeks).

Scales about 3 mm. broad; nuclear area more or less rugose.

Distichodus brevipinnis Günther. Fashoda, White Nile (Loat).

Scales little broader than long, shaped as in *D. niloticus*, but larger.

Distichodus niloticus Linnæus. Fashoda, White Nile (Loat).

Distichodus rostratus Günther. Gondokoro, White Nile (Loat).

Scales quite as in *D. niloticus*; dermal pigment-spots also the same.

Distichodus lusosso Schilthuis. Banzyville, Ubangi (Capt. Royaux).

Scales small, less than 3 mm. diameter; subapical field broadly rugulose.

Distichodus mossambicus Peters. Loangwa River, N. W. Rhodesia (S. A. Neave).

Nuclear area very broadly rugulose; a subdorsal scale is broader in proportion to its length than one from near the lateral line.

Distichodus sexfasciatus Boulenger. Coquilhatville, Upper Congo (Delhez).

Scale rather broad; apical field with radiating grooves.

Distichodus notospilus Günther. Kribi River, Cameroon (*G. L. Bates*); Komadekke, Ogowe (*W. J. Ansorge*).

The Kribi R. specimen has the largest scales I have seen in this genus, about 8.5 mm. long and 10.5 broad.

Judging from the general characters of the fishes, and especially perhaps from the development of the maxillary, we may infer that the Hydrocyoninae, a carnivorous group, have given rise to the herbivorous Citharininae. Using similar criteria, however, it would seem that the herbivorous Distichodontinae had given rise to the carnivorous Ichthyoborinae.

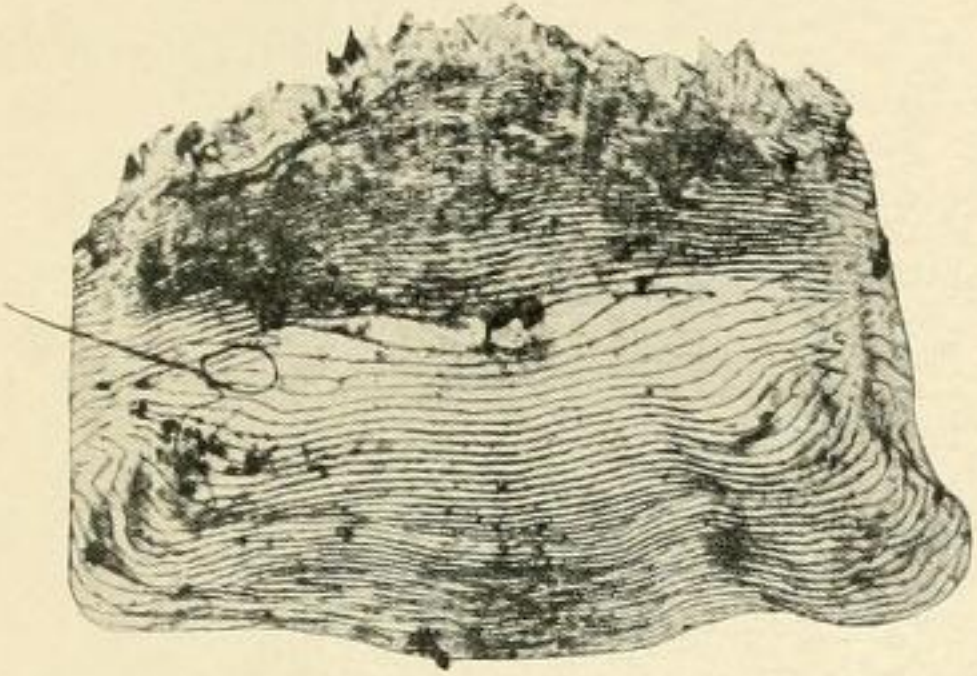
EXPLANATION OF PLATES

PLATE 1.

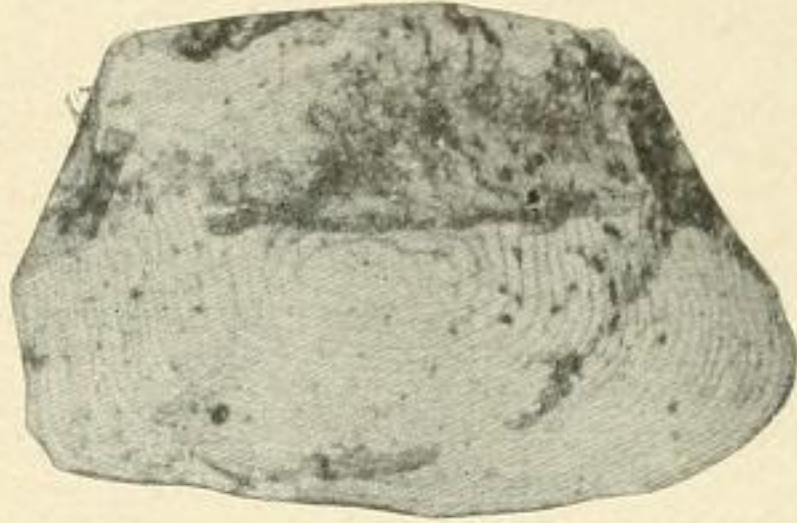
- FIG. 1. *Scomber chrysozonus*. Massauah. British Museum. Gill rakers very long.
- FIG. 2. *Scomber pneumatophorus*. Table Bay, Cape of Good Hope. = *colias* = *japonicus*. British Museum.
- FIG. 3. *Tilapia nilotica*. Birket Karûn, Fayoum. British Museum.
- FIG. 4. *Alestes sadleri*. Entebbe. Lake Victoria (Degen). British Museum.
- FIG. 5. *Micralestes holargyreus* Günther. Boma (Delhez). British Museum.
- FIG. 6. *Petersius caudalis*. Boma (Delhez). British Museum.

PLATE 2.

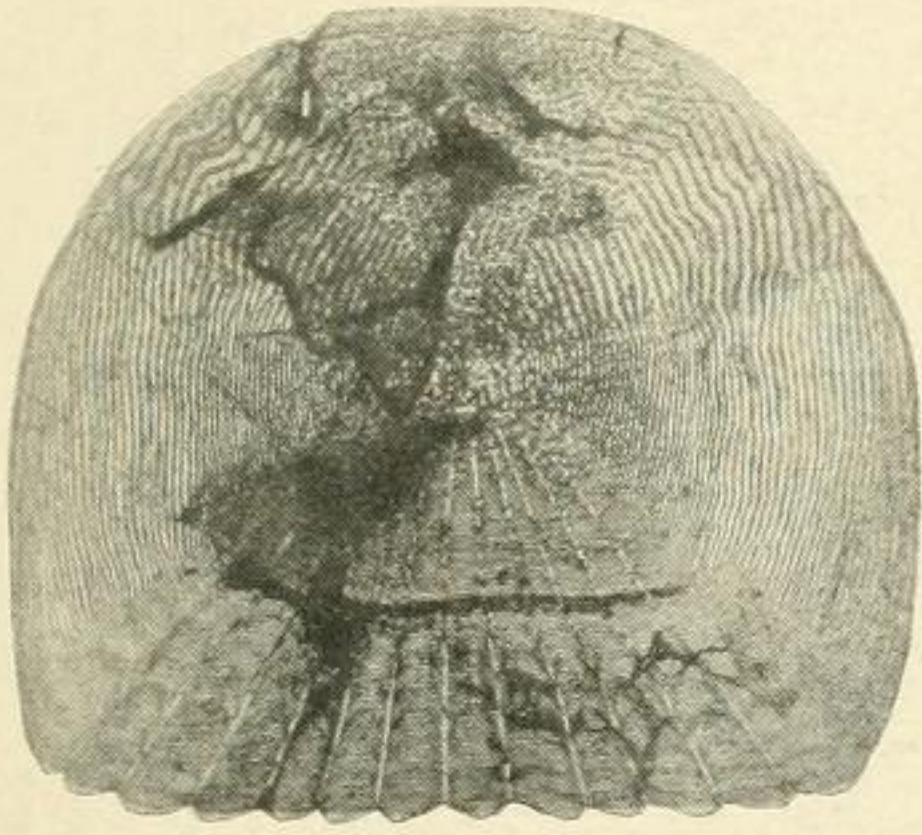
- FIG. 1. *Citharidium ansorgii*. Lake Oguta. S. Nigeria (Ansorge). British Museum.
- FIG. 2. *Citharinus congicus*. Bololo. Congo (Grenfell). British Museum.
- FIG. 3. *Eugnathichthys eetveldii* Blgr. Monsembe. Upper Congo (J. H. Weeks). British Museum.
- FIG. 4. *Xenocharax spilurus*. Ibali. Lake Leopold II (Delhez). British Museum.
- FIG. 5. *Distichodus antonii*. Monsembe. Upper Congo (Weeks). British Museum.
- FIG. 6. *Distichodus sexfasciatus*. Coquilhatville. Upper Congo (Delhez). British Museum.
- FIG. 7. *Distichodus notospilus*. Komadekke. Ogowe (W. J. Ansorge). British Museum.



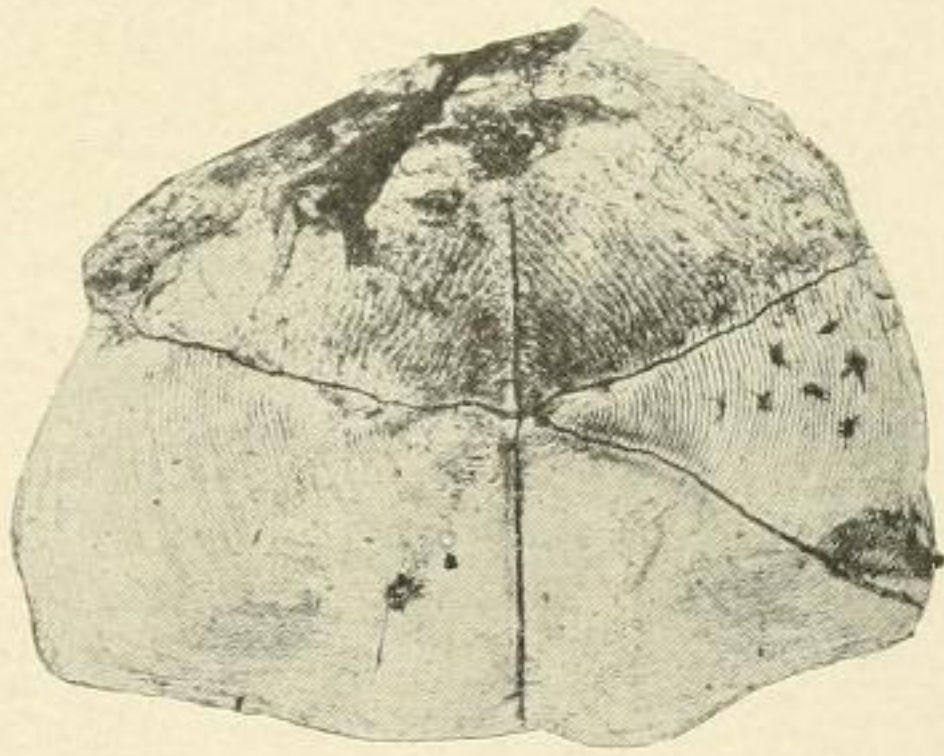
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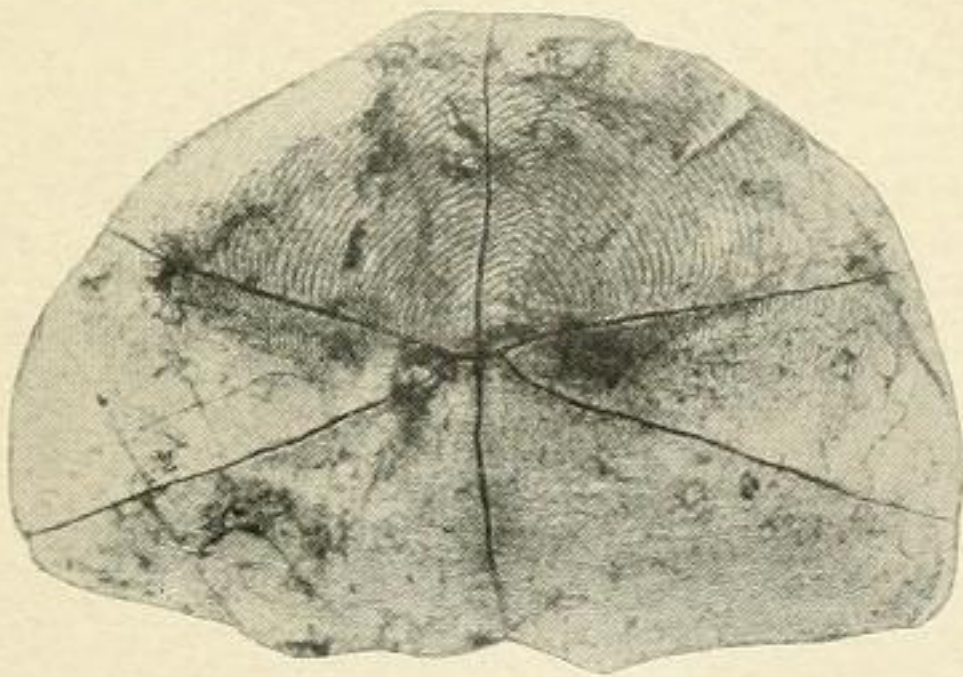
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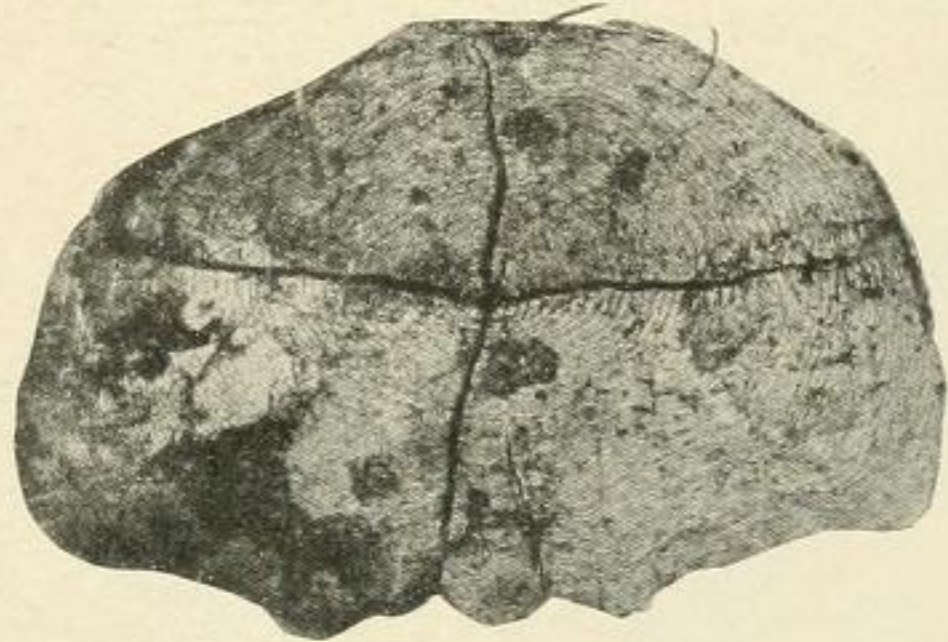
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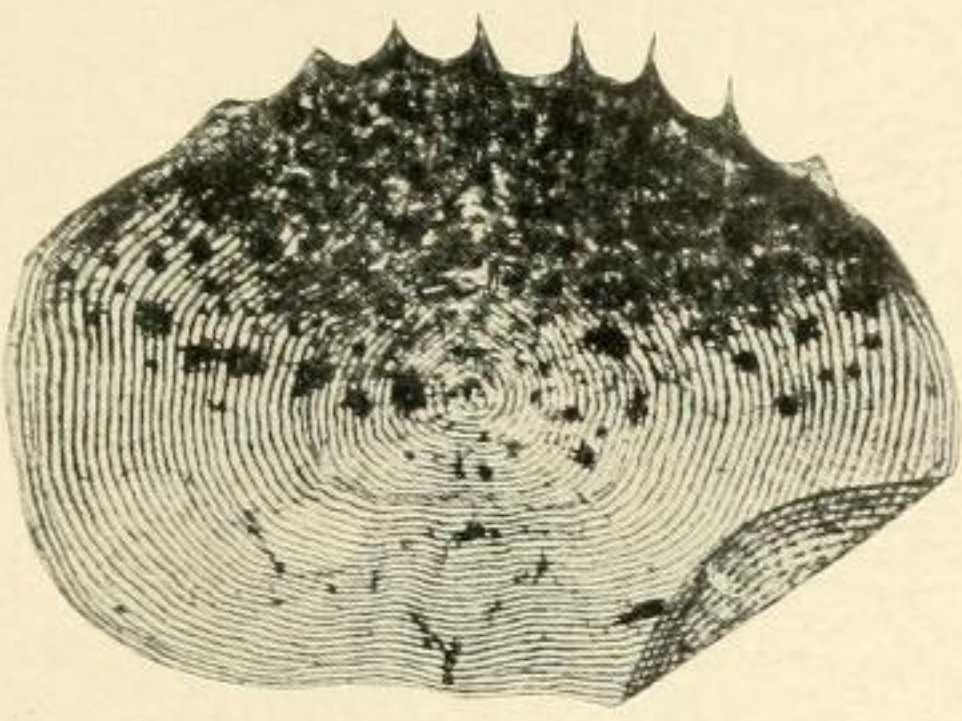


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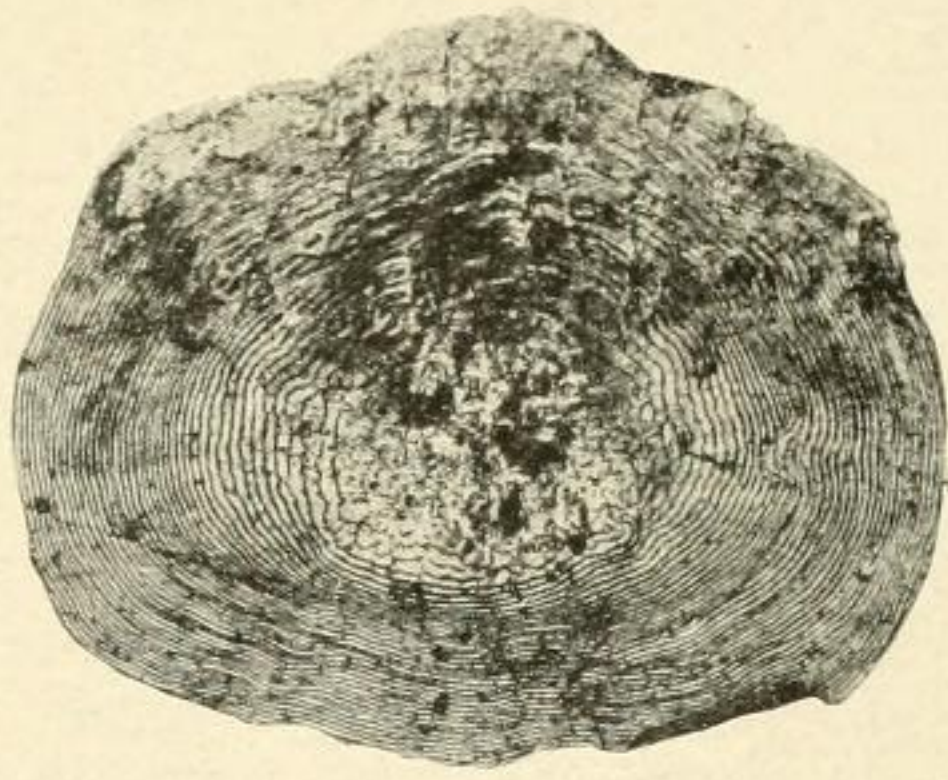


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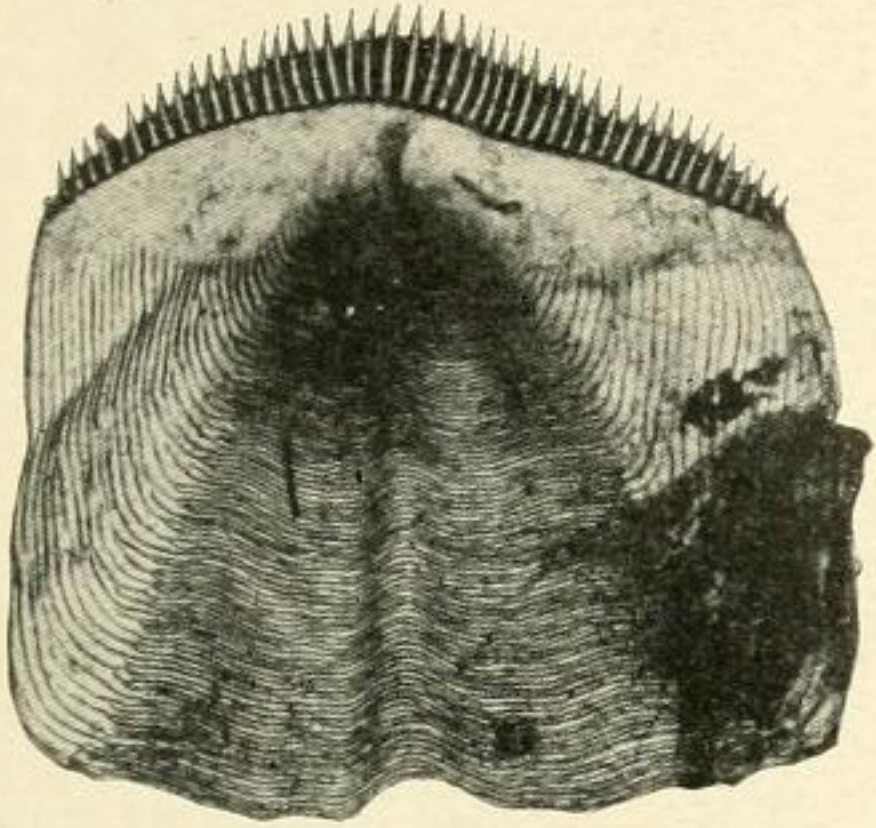
SCALES OF AFRICAN FISHES



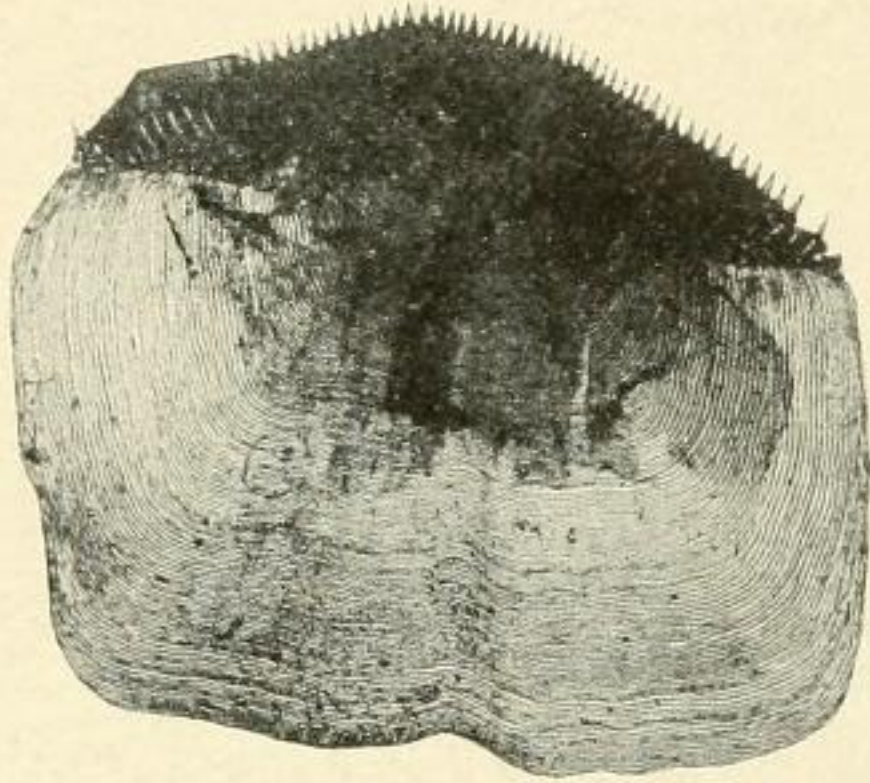
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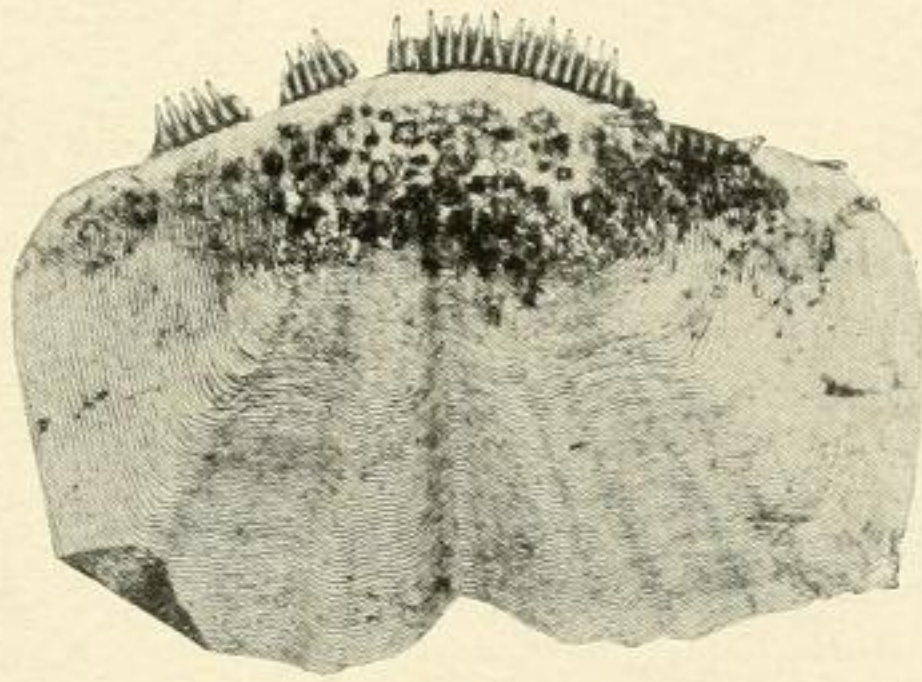
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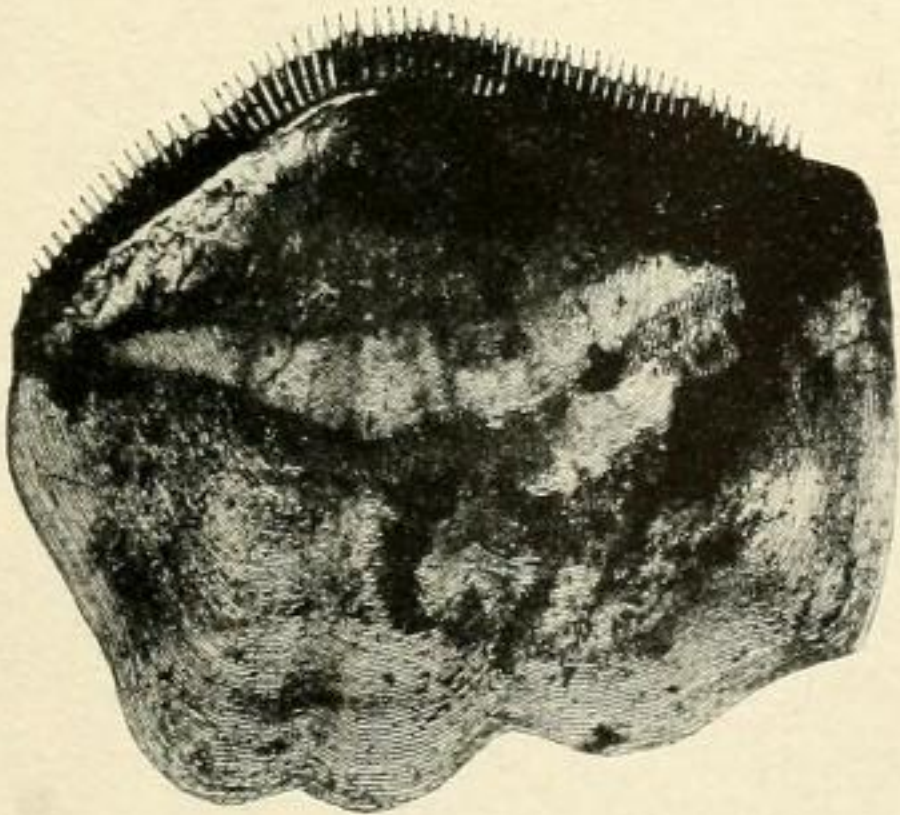
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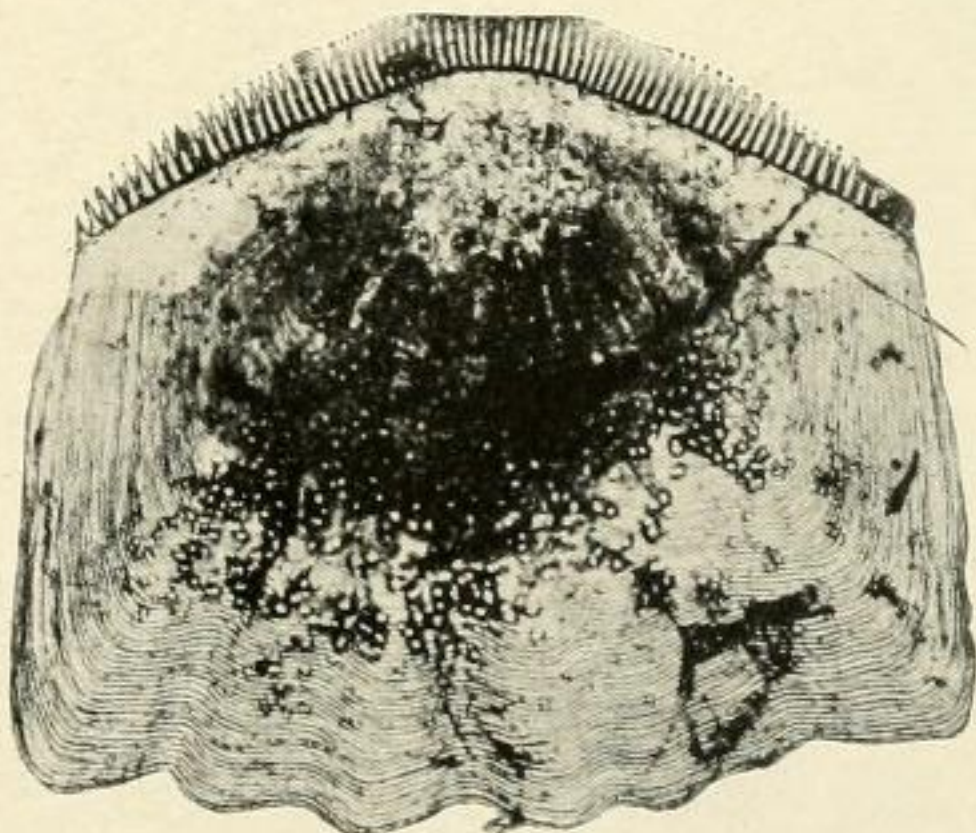
4



5



6



7

SCALES OF AFRICAN FISHES