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BLIND CATFISHES FROM ARTESIAN WATERS
OF TEXAS*

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DURING the course of a collecting trip to the western and south-western United States in 1938, the senior author visited the Witte Memorial Museum at San Antonio, Texas. Mrs. Ellen S. Quillin, the director of that institution, made available for his examination two blind catfishes (Ameiuridae) which had been pumped from deep artesian wells in the vicinity of San Antonio. Subsequently, these specimens were loaned to the Museum of Zoology. We are greatly indebted to Mrs. Quillin for placing these specimens in our hands for study. Both are now in the Witte Memorial Museum.

One of the specimens is the second known example of the remarkably specialized *Trogloglanis pattersoni* Eigenmann. The other proves to represent a distinct new genus and species apparently allied to *Pilodictis olivaris*. Other blind catfishes have been taken, but are not available. One from the artesian well of the Alamo Dressed Beef Company was presented to Witte Memorial Museum (Accession No. 25.193.37.G) but could not be found. Still others appear not to have been preserved. Thus, a blind fish from an artesian well was reported

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by Mrs. R. P. Persyn in the *San Antonio Light*, September 7, 1929. Mr. Josef Boecke, who collected one of the specimens described below, told us on June 3, 1938, that he had seen about twenty blind, pink catfish in the irrigation ditches fed by his artesian well, which is 1000 feet deep. Very sluggish, they were easily caught by hand. The last one seen by him was caught in June, 1934. He knew of another that came from an artesian well 1250 feet deep, west of San Antonio. It is much to be hoped that additional specimens will be preserved.

The two blindcats now known from the subterranean waters about San Antonio are completely devoid of external eyes and skin pigment. That both belong to the catfish group confirms the view (Norman, 1926: 325-29; Hubbs, 1938: 266) that catfishes are particularly well represented in the subterranean fauna. *Satan eurystomus* adds not only a new genus and species to the list of blind, depigmented cave fishes, but also another line of evolution of such types. It seems to have been derived from an ancestor of *Pilodictis olivaris*, whereas *Trogloglanis pattersoni* appears to have been evolved from the *Ameiurus* type. *Satan* and *Trogloglanis* are clearly members of the North American fresh-water catfish family Ameiuridae.

The habitat of the blindcats of the San Antonio region is amazing. The specimens have come from artesian wells 1000 to 1250 feet deep. It is virtually certain that they have been derived from the chief water-bearing stratum of the region. This is the Edwards Limestone Formation of Comanche (Lower Cretaceous) age (Livingston, Sayre, and White, 1936). In the vicinity of San Antonio the top of this formation lies 400 to 1000 feet underground. Like the other formations of the region the Edwards Limestone dips toward the coast. In the southernmost part of Bexar County it lies about 3000 feet below the land surface. Farther northwest, on the Edwards Plateau, it lies at the surface. There are obviously open channels through the limestone for the artesian head closely follows precipitation. The population of the great subterranean depths by the ancestors of these catfishes is, therefore, explainable. Livingston, Sayre, and White (1936: 73) wrote:

Extensive exploration by wells in this reservoir in Bexar County has shown that under large areas the limestone is traversed by an intricate system of openings. In some places the openings are small, apparently being confined to joint planes and fissures. In others they consist of solution channels of varying sizes, the largest good-sized caverns.

Since, prior to the drilling of the wells, the water in the Edwards Limestone reached the surface in large springs along Balcones Fault, and since the water in the wells now reaches to or nearly to the surface, it is obvious that the blindcats live under great hydrostatic pressure. In correlation with this habitat condition the air bladder in both species appears to have become obsolete.

Artesian waters in three prefectures of Japan have yielded a fish that is unrelated to the blindcats of Texas but parallels them in its modifications for subterranean existence. It is a member of the essentially marine family Gobiidae. Along with a similar cave form, it appears to be closely related to a common Japanese littoral goby, *Luciogobius guttatus*. The 2 subterranean, presumably fresh-water forms were very briefly described by Tomiyama (1936: 51-52, Figs. 10C-D) as variations of what he called *Luciogobius guttatus guttatus*. Regan (1941) more plausibly treated them, on the basis of Tomiyama's account, as distinct species, which he named *Luciogobius pallidus* (from the artesian wells) and *L. albus* (from a cave). They might be regarded as comprising a special genus, for they differ from the littoral gobies of the genus *Luciogobius* not only in characters associated with their dark habitats but also in an apparently trenchant feature, the lack of free pectoral rays. The cave form was described as an albino with more or less degenerate eyes. The artesian form was said to be paler and to have the eyes covered by skin. The 2 differ sharply from one another as well as from the 2 known littoral species of *Luciogobius* in body, head, and fin proportions.

This artesian-water goby and the 2 blindcats of Texas are apparently the only blind fishes that are known to inhabit artesian waters. Various other species have been reported from the outflows from artesian wells, particularly in arid

regions. Some of the published accounts (listed on pages 406 and 423 in Volume III of Dean's *Bibliography of Fishes*), as well as a number of verbal reports from residents in the Great Basin, claim that the fish issued from the ground. The species concerned, with the exception of the 3 kinds under discussion, are, however, eyed and pigmented. It seems probable that their isolated distribution is attributable to some channel of dispersal other than an underground connection. Occasional surface flows of flood water readily explain some of the cases investigated afield.

Satan, new genus

Orthotype, *Satan eurystomus*, new species.

This genus is sharply differentiated from other genera of ameiurid catfishes except *Trogloglanis* by the complete absence of eyes, the obsolescence of the air bladder, and the lack of pigmentation. Despite their similarity in degenerative and adaptive features associated with subterranean life, *Satan* and *Trogloglanis* are strikingly different in many characters (Table I). Although the relationship of neither genus is fully certain, it is apparent that they represent separate evolutionary lines and that their similarities are due to convergence rather than to a common origin from a cave-adapted ancestor. *Satan* is much less modified from the surface-living ameiurids than is *Trogloglanis*. From *Ameiurus*, the presumed ancestor of *Trogloglanis*, *Satan* differs in the absence of eyes, of pigmentation, and of air bladder, in the increased size and development of the lateral line canals and pores on the head, in the reduced size of the narial apertures, in the excessive development of the adipose fin, in the reduced length of the intestine, in the more flattened and trapezoidal shape of the head, and in the broad overlapping of the branchiostegal membranes.

In superficial characters *Satan* is most closely approached by *Pilodictis*. These genera have a very similar body form, with a greatly depressed head, wide transverse mouth, slender body, and a long and flaring adipose fin. The branchiostegal mem-

TABLE I
COMPARISON OF THE TWO BLIND CATFISHES FROM TEXAS

Character	<i>Satan eurystomus</i>	<i>Trogloglanis pattersoni</i>
Teeth on jaws	Well developed, in villiform bands	None
Jaws	Strong	Papery thin
Lower jaw	Arched, horizontal, covering premaxillary teeth	Straight and transverse, curved upward into mouth, entirely behind broad premaxillaries
Mouth	Transverse	Greatly inverted
Mouth, as seen from below	A gently arched slit	Open, semielliptical
Mouth opening inside ...	Scarcely restricted, more than half width of head	Greatly restricted, less than one-third width of head
End of gape	Horizontal, entirely below base of maxillary barbel	Sharply curved upward behind base of maxillary barbel
Lip at corner of gape	Thick, exposed	Thin, concealed
Nasal and maxillary barbels	Maxillary barbel very much the thicker and longer	Subequal in thickness and length
Mental barbels	Outer much thicker and longer than inner	Outer little thicker or longer than inner
Anterior nostril	A narrow tube	Broader, with a posterior flap
Posterior nostril	Small, about one-tenth internarial space; with lateral walls at base of barbel	Large, about one-fourth internarial space; lateral rim scarcely elevated
Gular fold	V-shaped	Obsolescent
Branchiostegal membranes	Broadly overlapping	Not overlapping
Angle of shoulder girdle, from below	About 50°	About 110°
Edge of shoulder girdle in front of scapular process	Scarcely arched	Strongly arched
Outer edge of testis ...	Finely ciliate	Weakly and sparsely lobulate
Epidermis	Velvety, easily rubbed off in preservation; hairlike cilia scarcely developed	Heavily beset with fine cilia and scattered coarse ones
Extent of visible lateral line	To below first dorsal or interdorsal space	Nearly to end of adipose dorsal

TABLE I (Cont.)

Character	<i>Satan eurystomus</i>	<i>Trogloglanis pattersoni</i>
Lateral line	In segments with pores at either end	Forming a keel (sub-continuous anteriorly), without well-defined pores
Lateral line pores on head	Medium to large, averaging about as large as posterior nostril; none tubular	Minute, very much smaller than either nostril; mostly in tubelets
Pore at front base of each nasal barbel	Lacking	Present
Anterior pair of mandibular pores	Opening into a common fossa	Widely separated
Snout	Greatly depressed and flat	Little depressed, broadly rounded in contour
Form of head contours from above	Isosceles trapezoid	Semioval
Free edge of rays at front margin of anal and pelvic	With very fine antrorse spinulations, several per segment	Smooth
Rays in dorsal, anal, pectoral, and pelvic fins	More numerous	Less numerous

branes are well separated and often overlap in *Pilodictis*, which in this respect furnishes, with *Istlarius*, the closest approach to the wide overlap seen in the blind genus. *Satan* and *Pilodictis* differ trenchantly, not only in those features that adapt *Satan* to life underground but also in the lack of the backward projections of the premaxillary tooth band in *Satan*, a well-developed feature in *Pilodictis*. This character varies, too, in the surface forms, since in addition to *Pilodictis* such projections occur in *Noturus*, a relative of *Schilbeodes* and, to a less extreme degree, in *Istlarius*, which is related to *Ictalurus*. In the Pimelodidae also some genera have and others lack the projections. In *Satan* the lower jaw is slightly included, whereas in *Pilodictis* it projects beyond the upper jaw, but *Satan* approaches *Pilodictis* in this character more closely than do other ameiriurids.

Because of these similarities, it is suggested that *Satan* and *Pilodictis* may have had a distant common ancestry. *Pilodictis olivaris* is widely distributed in the rivers of Texas today. It is a secretive, negatively phototropic species that seeks retreat in undercut banks or beneath flat boulders, stumps, logs, or other objects. A species of such habits and with well-developed tactile senses would be expected to work into underground waters if available. The abundance of small creatures in the subterranean waters of the San Antonio area (Eigenmann, 1919: 397) would provide an adequate food supply, and subsequent modification of such an intruding population would, as usual, result in depigmentation, loss of vision, and increased development of some sense organs.

The backward projections of the premaxillary tooth band are probably to be regarded as primitive. In this respect *Pilodictis* may be more generalized than *Satan*, as it assuredly is in pigmentation, in the development of eyes and air bladder, and in the structure of the sensory system on the body. The wide separation and broad overlap of the branchiostegal membranes in *Satan* is more extreme than in other genera of ameiriids and is probably to be considered a generalized character. A seemingly parallel situation—the retention by a specialized cave fish of a primitive character that has become modified in recent surface-living relatives—has been noted by Eigenmann in the Amblyopsidae. Pelvic fins are retained in the cave-living *Amblyopsis*, whereas its closest relative in surface waters, *Chologaster*, has lost them. *Satan*, in all probability, was derived from some now extinct surface-living ameiriid not greatly different in fundamental characters from *Pilodictis*.

Certainly, neither *Satan curystomus* nor *Trogloglanis paterstoni* is to be regarded as an immediate derivative or subspecies of its eyed ancestor, as *Typhlobagrus kronei* is supposed by Pavan (1946) to be related to *Pimelodella transitoria* or *P. lateristriga*.

WIDEMOUTH BLINDCAT

Satan eurystomus, new species

(Plate I, Figs. 1-3)

The holotype (Witte Memorial Museum, San Antonio, Texas, Accession No. 31.P.16.5) is an immature male, 68.7 mm. in standard length. It was collected near San Antonio and came from an artesian well 1250 feet deep. It was the gift of William Kempin.

Proportional measurements of the holotype, the only known specimen, are presented in Table II, and most features of body form and external anatomy are beautifully illustrated in the drawings (Plate I) prepared by Miss Grace Eager, accomplished staff artist of the Museum of Zoology. Many of the salient structural characters are indicated in the comparison with *Trogloglanis pattersoni* (Table I).

In common with most other blind, subterranean fishes, the lateral line canals and pores of the head are excessively developed. Two large pores open just behind the head, at the origin of the lateral line. The upper, more anterior one is almost level with the 2 pores comprising the straight part of the lateral line on the posterior part of the head. There are 12 large operculomandibular pores. The anteriormost pore on the mandible opens close to its fellow of the opposite side in a median transversely oval pit. A pore lies behind the eye position. Another is situated above and behind this pore. Of the 5 or 6 pores in the infraorbital series, the anterior 3 or 4 form a nearly horizontal line behind the anterior nostril. On each side there are 1 interorbital, 2 nasals, and 1 prenasal. No supratemporal canal or pores are visible. The lateral line extends to below dorsal or to below interdorsal space. It has 3 elongate pores in a short anterior tube, and behind this 5 to 9 short separated sections of tube, each with a pore on either end. Sense organs in the form of low cones are conspicuous, particularly on the head and anterior trunk regions.

The nostrils are minute. The diameter of the anterior one is about 0.4 mm., only two-fifths the size of that in *T. pattersoni*.

There are 10 branchiostegal rays. The gill-rakers on the

TABLE II

PROPORTIONATE MEASUREMENTS OF *Satan eurystomus* (HOLOTYPE) AND *Trogloglanis pattersoni* FROM NEAR SAN ANTONIO, TEXAS, EXPRESSED AS THOUSANDTHS OF THE STANDARD LENGTH

For paired structures measurements were taken on both sides and averaged.

Measurement	<i>Satan eurystomus</i>	<i>Trogloglanis pattersoni</i>
Standard length (mm.)	68.7	68.3
Body depth below dorsal origin	201	220
Body depth above anal origin, to top of adipose	174	223
Caudal peduncle depth (over-all)	104	127
Caudal peduncle depth (muscle mass only)	83	83
Caudal peduncle length	154	194
Predorsal length	343	319
Length to adipose origin	524	599
Dorsal base	133	110
Interdorsal distance	44	189
Adipose fin, basal length	371	307
Adipose fin, length to tip	381	328
Adipose notch to caudal base	127	115
Anal origin to caudal base	485	376
Anal base	234	196
Pelvic insertion to anal origin	163	162
Length to pelvic insertion	475	502
Anus to anal origin	45	63
Dorsal fin height	266	257
Dorsal spine length	105	175
Longest dorsal ray	245	225
Adipose fin, vertical height	60	86
Caudal fin length		
To upper angle	245	244
To end of shortest ray		212
To lower angle	238	242
Anal fin, depressed length	284	254
Longest anal ray	167	169
Pelvic fin length	136	149
Pectoral fin length	228	219
Pectoral spine length	105	174
Length first pectoral branched ray beyond tip of spine	123	45
Between pectoral insertions	224	255
From inside of shoulder girdle to tip of humeral process	47	39
Between pelvic insertions	108	102
Between pelvic fins	28	33
Head length	309	271
Head width	225	266
Head depth at occiput	182	174

TABLE II (Cont.)

Measurement	<i>Satan eurystomus</i>	<i>Trogloglanis pattersoni</i>
Head depth at end of first third of projection of head length	94	132
Mouth width		
Gape, exterior	159	131
Least interior width	120	81
At base of maxillary barbels, behind upper lip	154	139
Snout tip to mandible tip	8	49
Snout tip to front of gill opening	104	129
Front of gill opening to line joining pectoral insertions	146	78
Length of barbels		
Nasal	86	210
Maxillary	329	202
Outer mental	142	145
Inner mental	88	137
Distance between posterior nostrils	81	61
Snout to posterior nostril	78	58
Mandibular tooth patch, length	9*
Premaxillary tooth patch		
Length	11*
Width	126*

* No teeth on jaws.

outer arch number $4 + 15 = 19$. They are slender and moderately long. The longest is about one-third as long as the distance between the posterior nostrils.

The premaxillaries bear a well-developed patch of villiform teeth which form a transverse band without backward projecting processes. The length of the band is 9 per cent of the width; there is no separation or constriction at the midline. The palate is toothless.

The first dorsal fin is high and somewhat pointed, with 1 rather weak spine and 7 branched rays (counting the last 2 elements as 1 ray). The anal is long and low, with 6 unbranched and 14 branched rays. Along the front margin of the anal fin the anterior rays bear several weak antrorse spinules per segment. Except for the marginal principal rays the caudal fin is mutilated distally, but the form of the remaining part of the fin suggests that it may have been slightly emarginate. There are 17 principal caudal rays; 13 procur-

rent rays above, of which at least 5 are segmented; and 16 procurrent rays below, of which at least 4 are segmented. Each pectoral fin has 10 branched rays and a single spine, which is smooth along its anterior edge and bears 8 to 10 serrations posteriorly. Each pelvic fin has 9 branched rays and 1 simple ray on its outer edge, which bears spinules like those at the front of the anal fin.

The intestine is relatively thick-walled and rather short, with one extra coil about one-third as wide as the mouth. The outer edge of the testis is finely fringed, as is usual in the family. No trace of an air bladder could be found. The body cavity is largely filled with adipose tissue.

Several notable differences in form between *S. eurystomus* and *T. pattersoni* are best indicated by angle measurements (taken as described by Hubbs, 1946). In *S. eurystomus* lines joining the insertions of the pectoral fins with the point of union of the branchiostegal membranes intersect at an angle of 71° ; those joining the pectoral insertion with the tip of the snout, at 51° . The angle formed by the edges of the shoulder girdle, as seen from below, is about 50° ; by the edges of the gular groove, 63° ; by lines joining the insertion of the pectorals and the corners of the mouth, 15° ; by the dorsal and ventral contours of the head, just behind the barbels, 25° ; and by the muzzle, in lateral profile, 21° .

Satan eurystomus signifies "wide-mouthed prince of darkness."

Trogloglanis Eigenmann

Orthotype.—*Trogloglanis pattersoni* Eigenmann.

This, the only previously known genus of the Ameiuridae that is wholly blind, depigmented, and subterranean, is the most sharply differentiated genus of the family. Most of its salient characteristics are given in Table I. The weak toothless mouth, much modified jaws, greatly restricted and internally situated mouth opening, foreshortened head, and obsolete air bladder, together with the modifications of the sensory system and of pigmentation, set this genus off as the most highly specialized of the Ameiuridae. Its distinctness was not fully appreciated by Eigenmann.

Eigenmann (1919: 398) suggested that *Trogloglanis* is a derivative of *Schilbeodes*. The similarity in form, in shortness of anal fin, and in certain other characters accords with this interpretation, but differentiation has proceeded so far that it is perhaps impossible to be certain of the relationships. In agreement with *Ameiurus*, as contrasted with *Schilbeodes*, the venom pore in the pectoral axil is lacking (it is present in the young only of *Ameiurus*) and the adipose fin, although large, is separated from the procurrent caudal rays. Derivation from *Ameiurus* appears to be most plausible.

Gronias nigrilabris Cope (1864: 231-32) has also been regarded as a blind cave catfish related to *Ameiurus*. The specimens, however, were caught in Conestoga Creek, Pennsylvania, and were assumed to have issued from limestone caves merely because the specimens had defective eyes. They were well pigmented and had an air bladder. We see no reason for thinking that the types of *Gronias nigrilabris* were other than specimens of *Ameiurus nebulosus nebulosus* (LeSueur) with eyes defective due to injury or some other cause. Such fish are not infrequently encountered. The serrated pectoral spine as well as the locality precludes the relationship with *Ameiurus melas* postulated by Jordan and Evermann (1896: 142). A figure of the type of *Gronias nigrilabris*, recently published by Fowler (1945: 55, Fig. 160), confirms our reference of *Gronias nigrilabris* to the synonymy of *Ameiurus nebulosus nebulosus*.

TOOTHLESS BLINDCAT

Trogloglanis pattersoni Eigenmann

(Plate I, Fig. 4)

Trogloglanis pattersoni.—Eigenmann, 1919: 397-400, Figs. 1-2 (original description; comparisons; artesian well, San Antonio, Texas). Norman, 1926: 328-29 (listed). Hubbs: 1938: 264 (listed).

The second known specimen of this species (Witte Memorial Museum, Accession No. 34.20.7.G) is an immature male, 68.3 mm. in standard length. It was caught in June, 1934, by Josef Boecke in a ditch fed by an artesian well on his ranch, $2\frac{3}{4}$ miles east and $1\frac{1}{4}$ miles north of the Alamo in San Antonio,

Texas. Proportional measurements of this specimen are presented in Table II, and the peculiar mouth structure is shown in Plate I, Figure 4. Most of the more striking characters are indicated in the comparison with *Satan eurystomus* (Table I).

Though well developed, especially on the head, the lateral line system is much less conspicuous than in *Satan eurystomus*. Between a slender tube at the front of the lateral line and the uppermost pore of the opercular series, but at a distinctly higher level, are 2 similar tubules. The more posterior of the 10 or 11 small operculomandibular pores are at the tips of minute tubes. The anteriormost pore on the mandible is well separated from its fellow of the other side. There is one similar pore behind the eye position, another above and slightly behind this, 5 or 6 in the infraorbital series, 2 interorbitals, 2 nasals, 1 prenasal, and 1 more at the front base of each nasal barbel. All these pores are very minute. Most of them open in small tubules. No supratemporal canal or pores are visible. The lateral line is developed to near the posterior end of the adipose fin, but is much interrupted posteriorly. Anteriorly, it consists of an irregularly lobate dermal keel, with mere traces of open tubes and pores.

The nostrils are of moderate size. The diameter of the anterior is about 1.0 mm. It is notably larger than in *S. eurystomus*.

There are at least 8 branchiostegal rays. The gill-rakers on the outer arch number $4 + 15 = 19$. They are slender, but very short. The longest is about one-seventh as long as the distance between the posterior nostrils.

The very delicate jaws as well as the bones of the palate are toothless.

The dorsal fin is high and somewhat pointed, with 1 long, well-developed spine and 5 branched rays. The anal, more or less semicircular in outline, has 4 unbranched and 11 branched rays. The outer ray is smooth. The caudal fin is weakly truncate, not convex posteriorly as shown in Eigenmann's figure (1919: 398, Fig. 1). In addition to the 17 principal caudal rays there are 13 procurrent rays above, of which 1 is

segmented, and 15 procurrent rays below, of which 3 are segmented. Each pectoral fin has 9 branched rays and a single strong spine, which is smooth along its anterior edge and bears 8 or 9 prominent serrations posteriorly. The pelvic fin of the right side has 1 simple ray on its outer edge, which is smooth, and 7 branched rays.

The intestine is rather thin-walled and is somewhat more coiled than it is in *S. eurystomus*. The outer edge of the testis bears a few weak, lobulate projections, rather than the fine fringe that is usually developed in the Ameiuridae. No air bladder could be found. The body cavity is largely filled with adipose tissue.

Lines joining the insertions of the pectoral fins with the point of union of the broadly connected branchiostegal membranes intersect at an angle of 108° ; those joining the pectoral insertions with the tip of the snout, at an angle of 68° . The angle formed by the edges of the shoulder girdle, as seen from below, is about 110° . The gular groove is obsolete. The angle formed by the lines joining the insertions of the pectorals and the corners of the mouth is 34° ; by the dorsal and ventral contours of the head, just behind the barbels, 24° ; and by the muzzle, in lateral profile, 46° .

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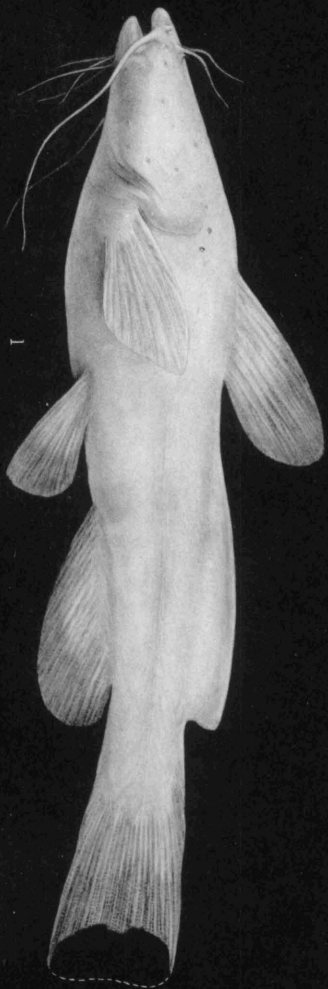
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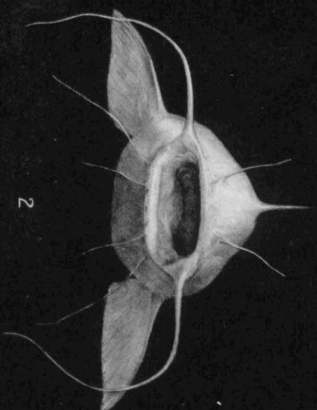
PLATE I

FIGS. 1-3. *Satan eurystomus*, holotype, in lateral, anterior and ventral aspects; standard length, 69 mm.

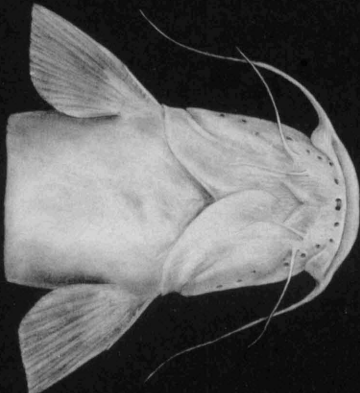
FIG. 4. *Trogloglanis pattersoni*: anteroventral aspect of the second known specimen; standard length, 68 mm.



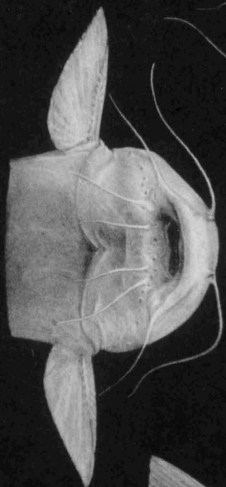
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2



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4

Grace Eagen

