The Comparative Anatomy of the Toothless Blindcat, *Trogloglanis pattersoni* Eigenmann, with a Phylogenetic Analysis of the Ictalurid Catfishes

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ABSTRACT

The skeletal and soft anatomy of *Trogloglanis pattersoni* Eigenmann are described and compared to other ictalurids. *Trogloglanis* is shown to possess a distinctive mosaic of relatively primitive and highly derived character states. Many of its features are paralleled in other troglobitic catfishes, some of its features are paedomorphic. Phylogenetic analysis leads to the following hypothesis of interrelationships. *Pylodictis* and *Satan* are sister groups, *Noturus* is monophyletic and is the sister group of *Prietella*, the subgenus *Amiurus* of *Ictalurus* is monophyletic and is the sister group of *Noturus* + *Prietella* + *Pylodictis* + *Satan*. In turn this large lineage is the sister group of *Trogloglanis*. The subgenus *Ictalurus* is monophyletic and is the sister group of all other living ictalurids. Geological and paleontological data suggest that *Trogloglanis* could not have evolved *in situ* before middle Eocene, but that its immediate epigean ancestors evolved by middle Oligocene.

INTRODUCTION

The evolution of cavernicoles from surface-living ancestors has been a minor but intriguing recurrent theme in the history of catfishes. Troglobitic catfishes are found in North America (Ictaluridae), South and Central America (Pimelodidae), Africa (Clariidae) and Asia (Clariidae) (Thines, 1969). Certain aspects of their biology have prompted authors to remark that the Siluriformes are pre-adapted for invasions of subterranean habitats (Eigenmann, 1919; Norman, 1926; C. L. Hubbs, 1938; C. Hubbs, 1971). Most catfishes are nocturnal, bottom dwellers; they rely more on olfactory, gustatory, tactile and electrical senses than on vision for social communications and food location (Todd et al., 1967; Bardach and Todd, 1970; Bardach and Atema, 1971; Reutter, 1978 and Alexander, 1965). That the visual sense is relatively unimportant in the lives of many catfishes is suggested by high frequencies of optically impaired individuals in populations of normally eyed species (Weisel and McLaurey, 1964; Pavan, 1946).

Within the Ictaluridae troglobitic species have evolved three times (Taylor, 1969; Lundberg, 1970, 1975a). *Prietella phreatophila* Carranza (1954), known from a single well in Coahuila, Mexico, is related to the genus *Noturus*. *Satan eurystomus* Hubbs and Bailey (1948) is a relative of *Pylodictis olivaris*. *Satan*, and the third blind ictalurid *Trogloglanis pattersoni* Eigenmann, are known only from deep (>305m) artesian wells and associated ditches near San Antonio,

Texas (Longley and Karnei, 1978). *Trogloglanis pattersoni*, the toothless blindcat, is the most aberrant member of the Ictaluridae (Figures 1,2). In 1919 Eigenmann based his original description of this species on a single specimen. Until 1977 only five additional individuals are known to have been deposited in museum research collections. Recently, through intensive collecting efforts of Glenn Longley and Henry Karnei, Jr. of Southwest Texas State University, twenty six specimens have been obtained (Longley and Karnei, 1978). As a result of its historic scarcity, *Trogloglanis pattersoni* is little known to science beyond readily observable features of its anatomy (Eigenmann, 1919; Hubbs and Bailey, 1947; Taylor, 1955, 1969; Suttkus, 1961; Lundberg and Baskin, 1969; Hubbs, 1971; Lundberg, 1970). Hypotheses on its evolutionary relationships have not been convincing mainly because of lack of data and little is known of the life history and habits of *Trogloglanis* in its native habitat (Longley and Karnei, 1978).

The present paper offers a more complete account of the anatomy of *Trogloglanis* than those cited above. The bony skeleton is described for the first time and the systematic position of this fish within the Ictaluridae is analyzed with comparative anatomical data. In previous studies of ictalurid phylogeny eight major living monophyletic groups have been recognized besides *Trogloglanis* (Taylor, 1969; Lundberg, 1970, 1972, 1975a): (1) *Ictalurus*[1], (*Ictalurus*), channel and blue catfishes, (2) *Ictalurus, (Amiurus)*[1], bullheads, (3) *Noturus, (Noturus)*, stonecat, (4) *Noturus, (Schilbeodes)*, madtoms, (5) *Noturus, (Rabida)*, madtoms, (6) *Prietella phreatophila*, Mexican blindcat, (7) *Pylodictis olivaris*, flathead catfish, and (8) *Satan eurystomus*, Widemouth blindcat. In addition, there are two extinct lineages of early Tertiary ictalurids: *Astephus* and *Hypsidoris*. These living and extinct lineages are believed interrelated by common ancestry according to the cladogram in Figure 3. A central task in this paper is to analyze the evidence which will allow *Trogloglanis* to be placed into this cladogram.

[1]Taylor (1954, p. 43) expanded the limits of the genus *Ictalurus* to include species referred to *Amiurus*. The basis for this was explicitly phenetic; Taylor cited *Ictalurus catus* as exhibiting intermediacy in several characters. For now 28 years virtually all North American ichthyologists and fisheries biologists have followed Taylor's recommendation. My studies of ictalurids (Lundberg, 1970, 1975a, and this paper) reopen the issue of the status of *Amiurus*. There is in fact a distinct "phenetic" gap between *Ictalurus* and *Amiurus*, with no species being intermediate in several characters which uniquely define each group. Paleontological data show that *Ictalurus* and *Amiurus* have been separate lineages since at least the Oligocene. Furthermore, phylogenetic analysis suggests that *Amiurus* are more closely related genealogically to ictalurids other than *Ictalurus*, i.e. the genus *Ictalurus* (*sensu* Taylor) is a non-monophyletic taxon. Even so, and despite personal "cladistic" inclinations in systematics, I opt for inertia here and retain *Amiurus* as a subgenus of *Ictalurus*. I recommend this conservative position until some further evidence is offered in support of the hypothesis on relationships presented herein.
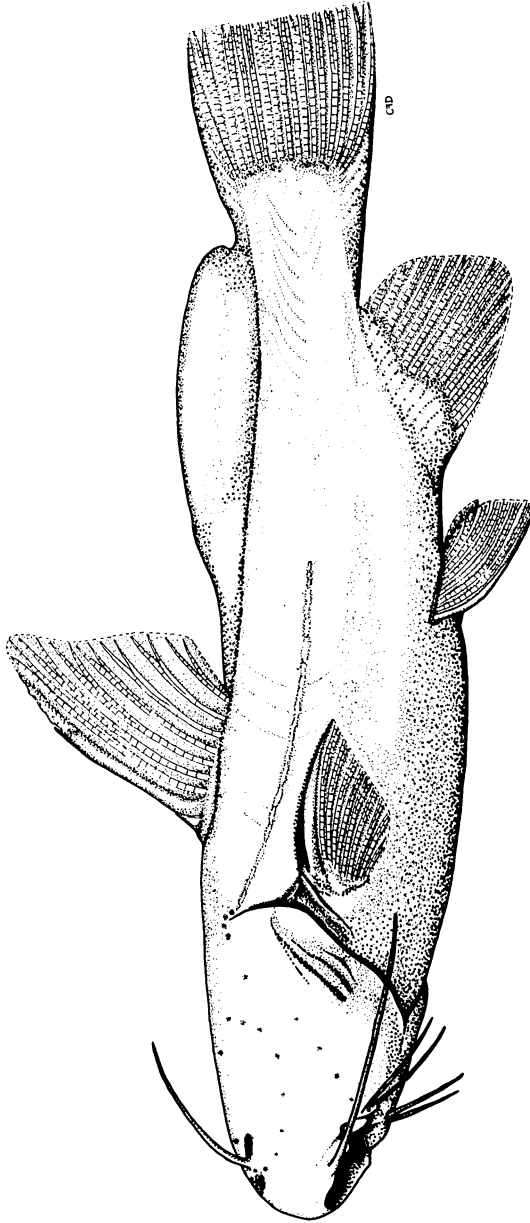
Fig. 1. *Trogloglanis pattersoni* Eigenmann. SIOH51-379-18A, 67 mm SL. Drawn by Carol Fletcher Daniels.
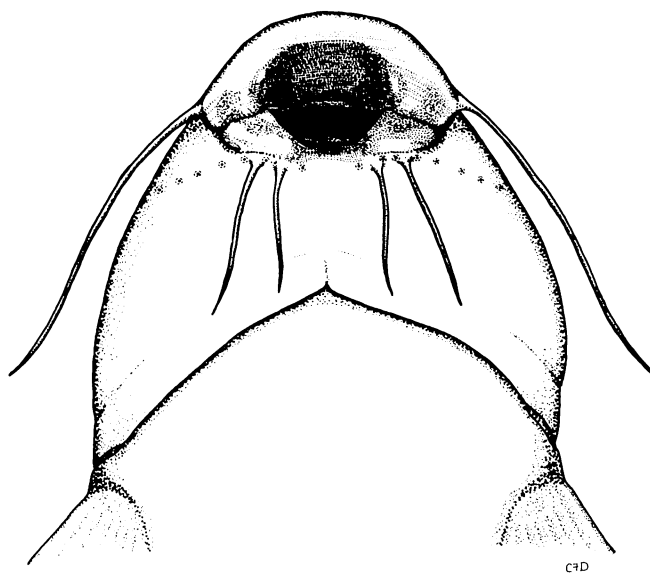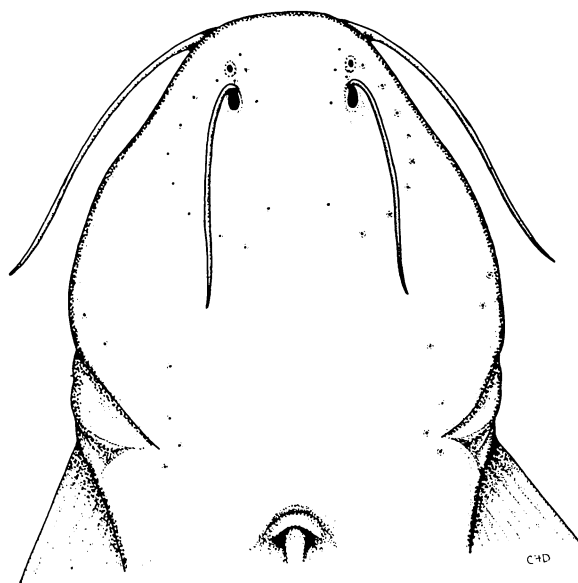
Fig. 2. *Trogloglanis pattersoni* Eigenmann SIOH51-379-18A, 67 mm SL. Top: Dorsal view of head. Bottom: Ventral view of head. Drawn by Carol Fletcher Daniels.
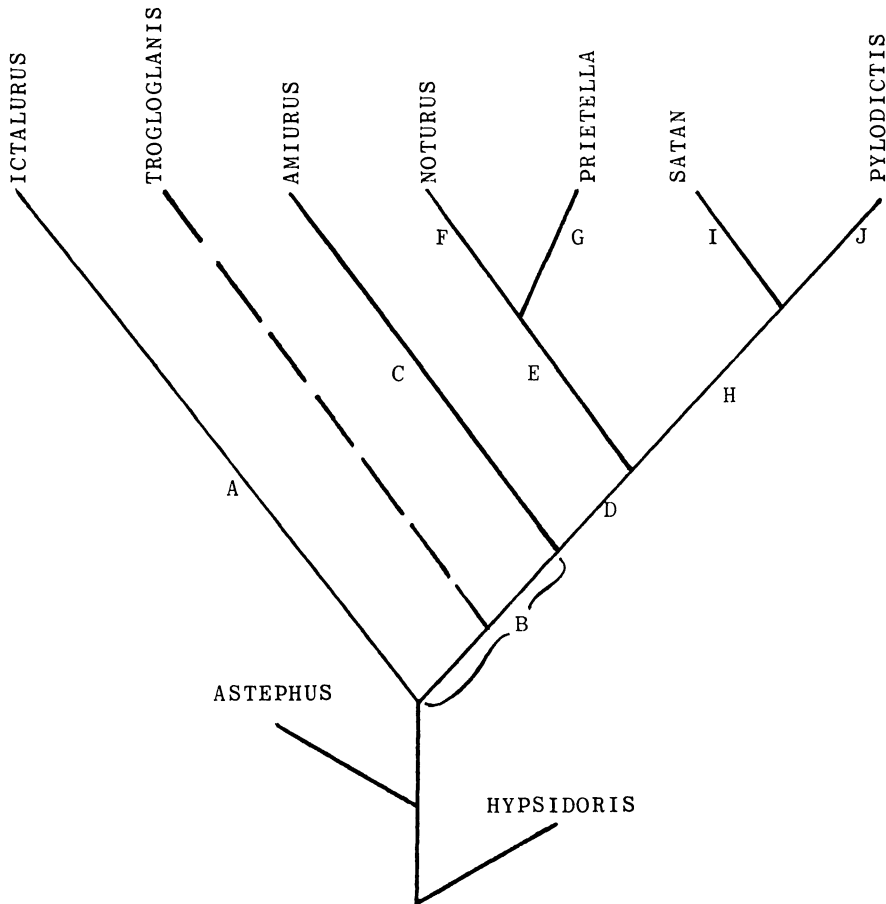
Fig. 3. Suggested genealogical relationships among the major subgroups of the Ictaluridae. Relationships shown by solid lines based on Lundberg (1970, 1975a). The relationship of *Trogloglanis* shown by dashed line is discussed in this paper. See text (pp. 00–00) for explanation of labelled intervals.

MATERIALS AND METHODS

Basic collection data on the known specimens of *Trogloglanis pattersoni* are given in Table 1. All specimens except those at Tulane and Southwest Texas University (Longley and Karnei, 1978) were used in this study. Comparative material included samples of nearly all recent and fossil species of ictalurids (see Lundberg, 1970, 1975a) and representatives of most other catfish families (see materials list in Lundberg and Baskin, 1969). Of three specimens of *Satan* known to science, only the type has been examined externally and with radiography. Although the details of the osteology of *Satan* remain to be worked out, enough is known to predict that it will be very close to *Pylodictis* in internal anatomy. Herein, it will be usually assumed

TABLE 1

DESCRIPTIVE DATA AND DISPOSITION OF THE SPECIMENS OF *TROGLOGLANIS PATTERSONI*

Specimen Number and Institution	Standard Length (Present)	Sex	Locality and Date of Collection	Key References
IU 15420 (California Academy of Science)	68.0 mm	♀	Texas, Bexar County, San Antonio, artesian well, 1918	Eigenmann, 1919
SIOH 51-350-18A (Scripps)	82.0 mm	♀	Texas, Bexar County, San Antonio, artesian well, 1944	— —
SIOH 51-379-18A (Scripps)	67.0 mm	♂	Texas, Bexar County, NE edge Von Ormy, O.R. Mitchell Ranch. Well 1,935 ft deep. 1951	— —
SIOH 51-379-18A (Scripps)	ca. 75 mm (alizarin stained specimen)	♀	"	— —
UMMZ 190921 (Univ. of Michigan) (originally Acc. No. 34.20.7.G, Witte Memorial Museum, San Antonio, Texas)	68.3 mm	♂	Texas, Bexar County, 2¾ miles E, 1¼ miles N of the Alamo, San Antonio, J. Boecke Ranch. Ditch fed by artesian well. 1934	Hubbs and Bailey, 1947 Taylor, 1955, 1969 Lundberg/Baskin, 1969 Lundberg, 1970
TU 10808 (Tulane)	68.6 mm	?	Texas, Bexar County, Von Ormy, O.R. Mitchell Ranch. Deep well. ca. 1955	Suttkus, 1961
26 specimens (Southwest Texas St. Univ.)	38.7–87.2 mm	1 ♂ 1 ♀	Texas, Bexar County, Von Ormy, Verstraeten Farm well 1,682 ft. deep and San Antonio, Artesia Well 1,319 ft. deep.	Longley and Karnei, 1978

that *Satan* matches *Pylodictis* in character states not otherwise known to differ. Future investigations may reveal errors in this, but these should concern the finer points of anatomy.

Unless otherwise noted, counts and measurements were made following the recommendations of Hubbs and Lagler (1958).

One specimen, SIOH 51-379-18A (♀), was stained with alizarin dissolved in 70% ethyl alcohol. Because of the fragile condition of the specimen no attempt was made to clear it with trypsin or KOH. Partial clearing was achieved by passing the fish through a series of glycerin solutions, and this was supplemented with dissection. All figures of the skeleton were made with the aid of a Wild M-5 dissecting microscope and camera lucida.

ESTIMATES OF SHRINKAGE.—In the course of study it was discovered that some of the specimens had shrunk while in preservative for many years. The apparent amounts of shrinkage were determined by comparing my present measurements with original measurements as reported in the literature. This shrinkage problem discouraged attempts to describe and compare the species in morphometric detail.

Assuming no error in mensuration and correspondence of technique among workers, there had been a marked shrinkage of at least two specimens. One suspects that this is somehow due to long term storage in alcohol. Hubbs and Bailey (1947) tabulated many proportional measurements on UMMZ 190921. They reported this specimen as 68.3mm SL. My 1976 measurement of this fish is 64.0mm, which yields 6.2% shrinkage in about 29 years. Furthermore, Eigenmann (1919) reported the total length of the type specimen as 85mm. One ray of the caudal fin remains nearly complete today and my measurement of the total length of this fish is 77.0mm. This difference of 8mm, again assuming no error, indicates a shrinkage of 9.4% in length in about 60 years.

More information on shrinkage of UMMZ 190921 is presented in Table 2. Of greatest importance is the obvious non-uniformity of the shrinkage estimates between body axes (compare values for length, width and depth measurements), and along a single axis (compare head length and caudal peduncle length shrinkage values). Also, shrinkage occurs within single, unjointed skeletal elements, e.g., the pectoral spine.

Short term shrinkage of formalin preserved fish is known to fishery biologists (Yeh and Hodson, 1975). The phenomenon of size diminution of museum specimens is not well understood, and long term studies are needed to determine more exact values than those hinted at above for a broad spectrum of fishes. One hopes that the values reported here are overestimates, but, at least until we know more, ichthyologists desiring to use measurements on old fish should exercise caution.

TABLE 2

SHRINKAGE AFTER 29 YEARS IN PRESERVATIVE OF ONE SPECIMEN
(UMMZ 190921) OF *TROGLOGLANIS PATTERSONI*, EIGENMANN.
THIS SPECIMEN WAS ORIGINALLY PRESERVED IN 1934.

Date of Measurement	Hubbs and Bailey 1947		Lundberg 1976		Shrinkage
	Measurement in Millimeters	Proportion (thousandths of standard length)	Measurement in Millimeters	Proportion (thousandths of standard length)	
Standard Length	68.3	—	64.0	—	6.2%
Caudal Peduncle Length	13.3	194	11.9	186	10.1%
Caudal Peduncle Depth	5.7	83	4.8	75	15.8%
Head Length	18.5	271	16.0	250	13.5%
Head Width	18.2	266	16.8	263	7.6%
Head Depth at Occiput	11.8	174	11.0	172	6.8%
Pectoral Spine Length	11.9	174	11.4	178	4.2%

ANCESTRAL AND DERIVED STATES OF CHARACTERS.—
In evolutionary morphology there is intrinsic interest in under-
standing pathways of character state change and in phylogenetic
analysis it is essential to understand such evolutionary trends. Only
relatively derived states shared among taxa can be used as positive
evidence for their relationship by common ancestry.

Criteria for assessing the direction of evolutionary trends have
been discussed by several authors (Maslin, 1952; Simpson, 1961;
Hennig, 1966; Mayr, 1969; Kluge and Farris, 1969; Lundberg, 1972,
1973; Nelson, 1978). In the present study the central criterion for
determining the primitive (ancestral) extremes of characters is the
character state most widespread among siluriforms (and other tele-
osts) outside of the Ictaluridae.

Fossil ictalurids are not given special weight in showing ances-
tral conditions relative to extant confamilials, because by outgroup
comparisons they appear to represent advanced side lineages, not
direct ancestors (Lundberg, 1975a). Arguments for primitiveness
involving ontogenetic precedence have not been given high weight.
The lineage of special interest here, *Trogloglanis*, is diminutive and
obviously regressed in many parts of its anatomy, thus making
paedomorphosis an important pattern in its evolution (see Hecht and
Edwards, 1976).

ABBREVIATIONS USED IN ILLUSTRATION LABELS.—
Ab?-adipose deposits; Ar-articular bone; aap-attachment scar of ad-
ductor arcus palatini muscle; ac-crest for attachment of outer layer of
adductor mandibularis muscle; afn-anterior cranial fontanelle; ah-
attachment crest of adductor hyomandibularis muscle; ams-attach-
ment scar of adductor mandibularis muscle; at-trough for dorsal
aorta; a3-attachment scar of inner (A3) layer of adductor mandi-
bularis muscle; Bb-basibranchials; Bo-basioccipital; Br-branchioste-
gal rays; b-osseous bridge over symplectic canal; bl-bony lamina; btsl-
osseous part of transcapular ligament; C-claustrum; Cb-ceratobran-
chials; Cc-Weberian complex centrum (fused centra 2–4); Ch-cerato-
hyal; Cl-cleithrum; Co-coracoid; Crb-cerebellum; c-cartilage; cp-
cartilaginous coronoid process; Dr-dentary; Ds-dorsal spine; d-poste-
rior dentations of pectoral spine; dfop-divided optic foramen; dlc-
dorsolateral crest of premaxilla; dsc-articulation facets on second
dorsal pterygiophore for dorsal spine; E-epural; Eb-epibranchials;
Eh-epihyal; En-endopterygoid; Ep-epioccipital; Ex-exoccipital; eb-
epiphyseal bar; F-frontal; Fb-forebrain; Fl-facial lobe; Fr-fin rays; fc-
canal through hyomandibular for passage of facial nerve (VII); fop-
optic nerve foramen; fso-foramen of superficial ophthalmic nerve; ftf-
trigeminofacialis foramen; Hb-hypobranchials; Hh-hypohyals; Hy-
hyomandibular; Hyp-hypural plates; hf-articulating facet for hyo-
mandibular; hp-anterior process of hyomandibular; I-intercalare; Ib-
infrapharyngobranchials; Ih-interhyal; Int-intestine; Iop-interoper-

cle; ioc-cranial exit of infraorbital sensory canal; k-coracoid keel; k'-secondary coracoid keel; kch-ceratohyal keel; L-lacrimal (first infra-orbital); Le-lateral ethmoid; Liv-liver; lap-attachment crest for leva-tor arcus palatini muscle; lg-ligament; lo-attachment crest of levator operculi muscle; Mpt-metapterygoid; Mx-maxilla; m-mental fora-men; mb-maxillary barbel core; mes-mesocoracoid arch; mn-foramen of the mandibular branch of the facial nerve; N-nasal; Np-nuchal plate; ns4-neural spine of vertebra 4; Ol-optic lobe; Op-opercle; Or-orbitosphenoid; ob-orbital foramen for passage of the deep ophthal-mic nerve; oc-articulating condyle for opercle; Pal-palatine; Par-parasphenoid; Ph-parhypural; Pmx-premaxilla; Pop-preopercle; Pr-prootic; Pt-pterotic; Pts-pterosphenoid; Ptt-posttemporal (com-pound); Ptt'-laterosensory part of posttemporal; Ptt''-laminar bone part of posttemporal; Pl-first pterygiophore of dorsal fin; pap-anterior processes of pelvic girdle; pc-posterior cartilaginous process of pelvic girdle; pcp-posterior cleithral process; per-perforations in premaxilla; pf-articulating facet for palatine; pfn-posterior cranial fontanelle; poc-cranial exit of preopercular sensory canal; Q-quad-rate; S-sphenotic; Sc-scaphium; Scl-supracleithrum; Se-supraethmoid; Sn-supraneural; Soc-supraoccipital; Sop-suprapreopercle; Spl-dorsal fin spinelet; Sto-stomach; s-sutures; sa-articulation groove of pectoral spine; sc-symplectic canal for passage of part of mandibular branch of facial nerve; scp-laterosensory canal pore; sec-supreethmoid cornua; sp-subpterotic process of supracleithrum; ss-lateral spine of sphenotic; Tp-tooth plate; Tr-tripus; t-foramina in nuchal plate for tendons of dorsal fin erector muscles; tp-transverse processes; Ub-urinary bladder; V-vertebra; Vl-vagal lobe; Vo-vomer; I-olfactory nerve; II-optic nerve; V-trigeminal nerve; VII-facial nerve; 2,3,4,5,6,7-numbered infraorbital bones.

ANATOMICAL DESCRIPTION AND COMPARISONS

EXTERNAL ANATOMY

SIZE.—*Trogloglanis* is a diminutive ictalurid as measured by standard length which varies from 38mm to 87mm (Table 1). These specimens, however, may not be fully grown; whereas the sexes are readily distinguished, the gonad structure suggests immaturity (p. 00). Only *Prietella phreatophila* and a few species of *Noturus* are smaller than *Trogloglanis*. *Trogloglanis* appears to be closest in body size to *Satan eurystomus*, and to several species of *Noturus*. All members of the genera *Ictalurus*, *Pylodictis*, *Astephus*, *Hypsidoris* and some *Noturus* attain a greater size than *Trogloglanis*.

Among catfishes in general, such small adult size, at least less than 100mm SL, is probably a derived feature but one subject to

considerable parallel evolution. Because of this, no special significance can be seen in body size as an indication of evolutionary relationship. Small body size is clearly an adaptive feature among cave-dwelling fishes, for which energe sources may be scarce (Huets, 1953).

SHAPE.—Some proportionate measurements of *Trogloglanis* are compared to representative ictalurids in Table 3. Longley and Karnei (1978) give comparable data on 26 additional *Trogloglanis* specimens. Their measurements show the same trends as those given here. In the first column it is seen that *Trogloglanis* has a relatively short predorsal length. Here *Trogloglanis* is closest to *Noturus gyrinus*, *Satan* and *Ictalurus punctatus*, whereas the bullheads (*I. catus* and *I. natalis*), other *Noturus* and especially *Pylodictis* have the dorsal fin placed relatively far caudad. Predorsal length has not been extensively investigated among catfishes so it is difficult to say if the relatively short condition is primitive or advanced. Regardless, since some well established groups of ictalurids (*Noturus*; *Pylodictis-Satan*) are not definitely characterized by either short or long predorsal measurement, the character has minimal systematic significance beyond its use as a descriptor of species.

Head shape varies greatly among ictalurids as in many other families of catfishes (Table 3). In most catfishes, including some ictalurids, the head is moderately elevated and slightly longer than wide. In the subgenus *Ictalurus* (particularly in immature individuals) the head is fairly long, narrow and elevated. In *Pylodictis*, *Satan*, many species of *Noturus*, and a few bullheads the head is moderately to strongly depressed (reflected somewhat in body depth measurement in Table 3). *Trogloglanis* has a very wide non-depressed head (Figures 1 and 2). The extreme width appears to be derived phylogenetically and is unique to *Trogloglanis* within its family. Poulson (1963) has noted that the heads of troglobitic amblyopsids are wider than in non-troglobites.

Depression of the head and anterior part of the body are related in ictalurids. *Pylodictis* and *Satan* are the most flattened North American catfishes. *Noturus* are intermediate, and except for the flathead bullheads (*Ictalurus platycephalus* and *I. brunneus*), the species of *Ictalurus* and *Trogloglanis* are deeper. The deeper shape is probably a shared primitive condition within the catfishes in general.

The caudal peduncle of *Trogloglanis* is relatively long and shallow (Table 3). The bullheads (subgenus *Amiurus*), and *Noturus* have much more elevated masses of caudal musculature. Overall, *Trogloglanis* is most like *Pylodictis* and *Satan* in caudal peduncle form but whether or not this is a shared advanced condition is unclear.

The dorsal and pectoral fin spines are relatively long in *Trogloglanis* and these spines are about equal in length to one another.

TABLE 3

PROPORTIONATE MEASUREMENTS OF *TROGLOGLANIS PATTERSONI* AND REPRESENTATIVES OF
OTHER ICTALURID GROUPS EXPRESSED AS THOUSANDTHS OF THE STANDARD LENGTH.
INDIVIDUAL MEASUREMENTS AND THE MEAN ARE GIVEN FOR *TROGLOGLANIS*.
DATA FOR UMMZ 190921, TU 10808 AND *SATAN EURYSTOMUS* COMPILED FROM
HUBBS AND BAILEY (1947) AND SUTTKUS (1961). MEAN AND RANGE GIVEN FOR
MEASUREMENTS OF ALL OTHER SPECIES. SEE TEXT FOR DISCUSSION

		Predorsal Length	Head Length	Head Width	Body Depth at Dorsal Origin	Caudal Peduncle Length	Caudal Peduncle Depth (muscle mass)	Dorsal Spine Length	Pectoral Spine Length
	UMMZ 190921	319	271	266	220	194	83	175	174
	IU 15240	294	243	272	180	175	103	171	179
Trogloglanis	SIOH 51-350-18A♀	358	316	288	202	158	90	167	136
pattersoni	SIOH 51-379-18A♂	334	277	276	207	143	84	—	—
	TU 10808	355	307	281	208	179	—	—	—
	MEAN	332	283	277	203	170	90	171	163
Ictalurus punctatus		356	250	182	204	146	90	140	150
(n = 5)		(320–390)	(240–260)	(170–200)	(160–240)	(140–160)	(70–100)	(110–160)	(110–170)
Ictalurus catus		384	272	234	265	172	114	162	170
(n = 5)		(380–400)	(260–280)	(230–240)	(240–310)	(160–180)	(110–120)	(150–170)	(160–180)
Ictalurus natalis		378	280	230	238	144	140	114	122
(n = 5)		(370–390)	(270–290)	(220–240)	(230–250)	(130–150)	(130–150)	(100–130)	(110–130)
Noturus insignis		366	258	226	198	203	128	82	122
(n = 5)		(350–380)	(250–270)	(220–240)	(180–210)	(190–230)	(120–130)	(70–90)	(100–130)
Noturus furiosus		410	286	256	186	192	116	132	202
(n = 5)		(390–440)	(260–300)	(250–260)	(160–200)	(170–210)	(110–120)	(110–160)	(180–240)
Noturus gyrinus		342	272	232	194	212	130	122	126
(n = 5)		(330–350)	(250–290)	(220–250)	(170–210)	(200–220)	(130,130)	(90–150)	(110–140)
Pylodictis olivaris		405	290	230	170	150	90	100	100
(n = 2)		(390–420)	(270–310)	(230,230)	(170,170)	(140–160)	(90, 90)	(90–110)	(90–110)
Satan eurystomus		350	323	233	188	153	83	140	105
(n = 3)		(339–367)	(309–342)	(225–244)	(168–201)	(144–161)		(105–186)	
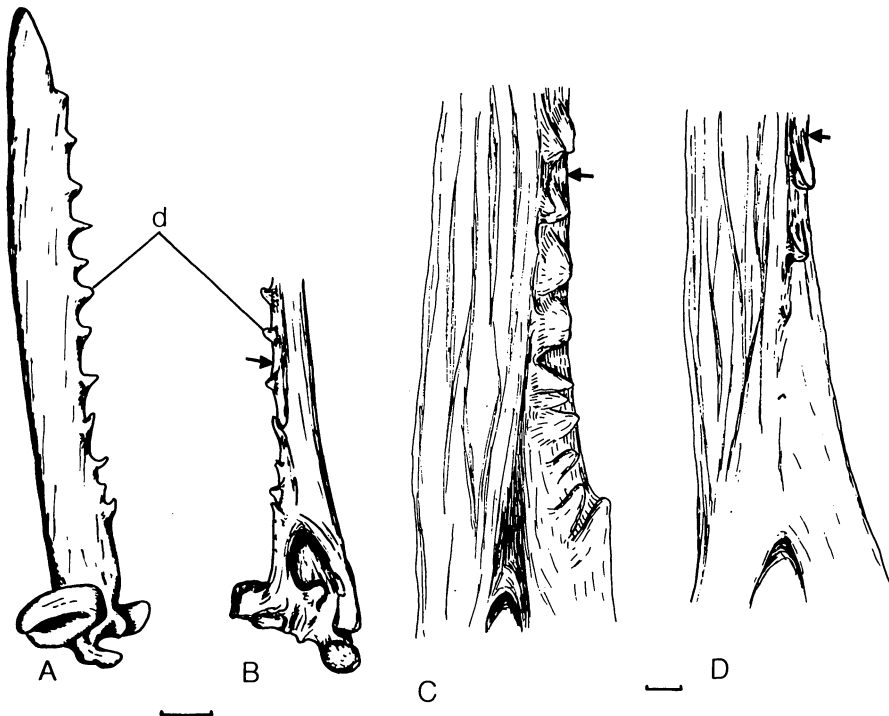
Fig. 4. A. Dorsal view of right pectoral spine of *Trogloglanis pattersoni* based on specimen SIOH51-379-18A, ♀. B. Posterior view of same. Scale for A and B 1mm. Posterior views of pectoral spine bases of C, *Ictalurus (Amiurus) catus*; D, *Ictalurus (Ictalurus) punctatus*, to show attachment sites of posterior dentations. Scale for C and D 5mm. Arrows point to dorsal edges of spines. For abbreviation see text (Materials and Methods).

Trogloglanis is most similar in these measurements to *I. catus* and *I. punctatus*. The extinct species *Hypsidoris farsonensis* has longer fin spines than any other ictalurid, about 220 thousandths of the standard length (Lundberg and Case, 1970). The relative length of the pectoral spine in *N. furiosus* (and other members of its species group) greatly exceeds that in other living ictalurids. Most species of *Noturus* possess a dorsal spine which is much shorter than the pectoral spine. Excessively long and short fin spines are probably derived conditions among catfishes. Within most large, well-marked groups of siluriforms, however, there is great variability in fin spine lengths so it appears that parallel evolution is commonplace. Near equality of dorsal and pectoral spine lengths such as found in *Trogloglanis*, because of its commonness throughout the Ictaluridae and other catfishes, is probably a primitive condition.

In body contours *Trogloglanis* (Figures 1 and 2), is basically like that of generalized siluriforms. The predorsal profile is gently convex, except for a more strongly curved snout. The postdorsal contour (without the adipose fin), the flanks and ventral contour of
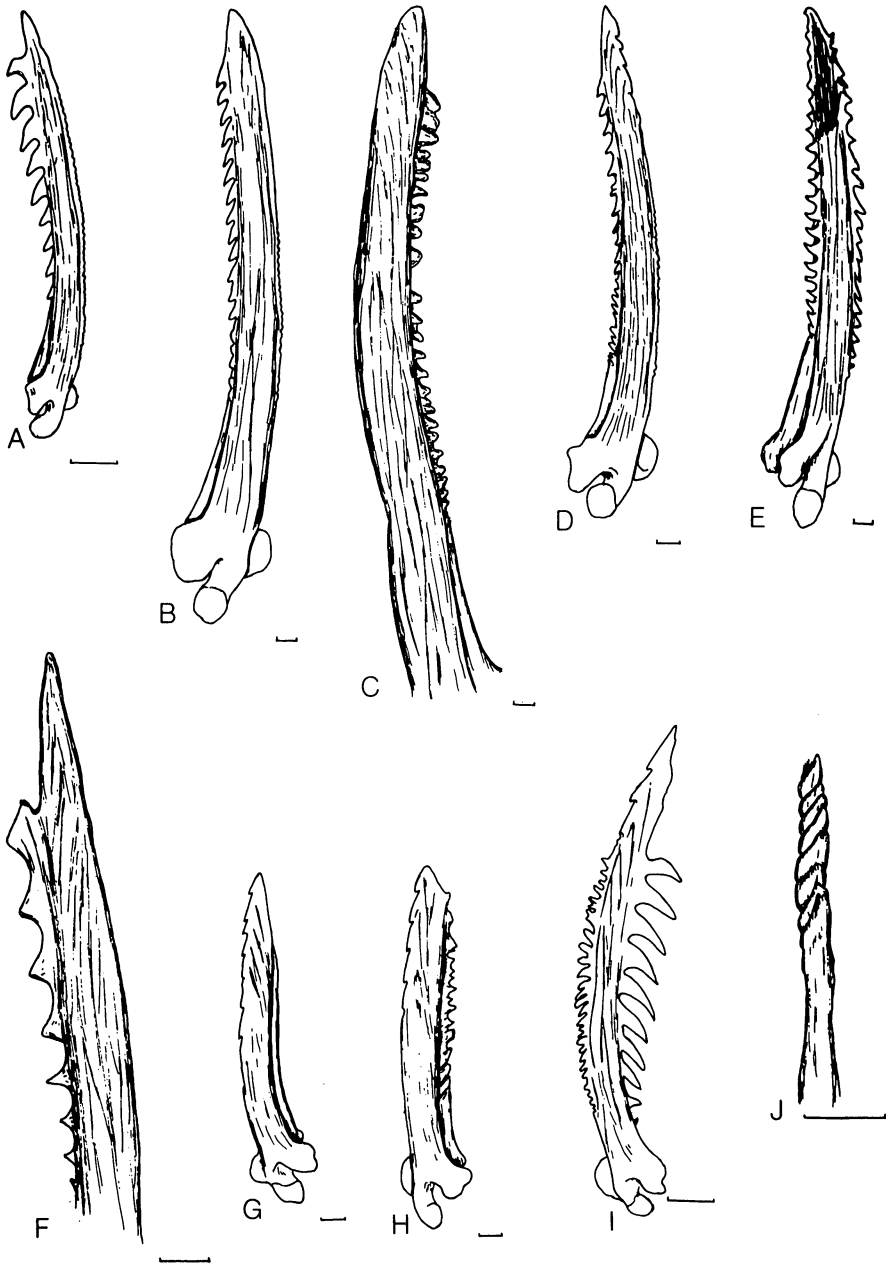
Fig. 5. Ventral views of pectoral spines. A–C *Ictalurus (Ictalurus) punctatus*, UMMZ 115991, 78301, 174667. D. *Ictalurus (Amiurus) catus*, UMMZ 186249-S-1. E. *Pylodictis olivaris*, UMMZ 169029-S-2. F. *Satan eurystomus*. G. *Noturus (Noturus) flavus*, UMMZ 126365-S-1. H. *Noturus (Schilbeodes) insignis*, UMMZ 186551-S-1. I. *Noturus (Rabida) stigmosus*, UMMZ 165841-S-1. J. *Prietella phreatophila*, UMMZ 173788. Scales for A–E, G–I 2mm; scales for F and J 1mm.

the tail taper evenly to the caudal fin. The head in cross-section is moderately arched above, flattened ventrally and strongly convex laterally.

MOUTH AND GILL MEMBRANE.—*Trogloglanis* has an odd funnel-like mouth, placed ventrally, below an overhanging snout (Figures 1 and 2B). The jaws are edentulous and permanently open as a result of mandibular foreshortening. Expanded upper and lower lips form fleshy pads, finely ornamented with transverse plicae. The upper lip is horizontal, the lower extends obliquely downward, away from the oral aperture. Except at the mouth angle, where there is a vertical fold, the lips are continuous with the head integument. The exterior expanse of the gape is wide, about 13% of the standard length as described by Hubbs and Bailey (1947). Internally, the mouth opening is greatly restricted with its internal width about 8% of the standard length. Oral valves are prominent, just inside the lips.

The structure of the oral apparatus of *Trogloglanis* is unique within the family Ictaluridae. The only feature that can be reasonably compared to other species is the mouth position. In most bullheads (subgenus *Amiurus*), most madtoms (*Noturus*), and *Satan* and *Astephus* the mouth is terminal. In *Pylodictis* the lower jaw protrudes beyond the upper. In the subgenus *Ictalurus* (see Taylor, 1969, p. 17), *Hypsidoris*, some *Noturus*, and the flathead bullheads (*I. brunneus* and *I. platycephalus*) the mouth is slightly to strongly subterminal. These catfishes, especially the channel and blue catfishes, come the closest to *Trogloglanis* within the family in having an inferior mouth. However, considering the vast differences in all other parts of oral anatomy these similarities may be superficial.

Outside of the Ictaluridae certain catfishes parallel *Trogloglanis* in general mouth form, but not in the loss of teeth. Examples are all loricariids, some sisorids (*Glyptosternum*, *Exostoma*, *Oreoglanis*) and some mochokids (*Chiloglanis* and *Euchilichthys*). These fishes have round, ventral mouths, surrounded by enlarged lips which may form a suction disk. It is not known if the oral apparatus of *Trogloglanis* is used as a suctorial organ. However, the food of *Trogloglanis* probably consists of minute particles taken in detritus from the substrate. A mud-like substance fills the stomach of some specimens examined by me. Longley and Karnei (1978) suggest that a subterranean fungus could be an important competent in the diet. The orientation and shape of the mouth is well suited to detritivory. The lips are probably hypertrophied tactile and tasting organs, and they may form a hood over loosened food particles which prevents them from being washed away during feeding.

The gular fold, typically a deep V-shaped fold between the mandibular and hyoidean arches in catfishes, is nearly obsolescent in *Trogloglanis* (Figure 2B), represented by a short, transverse groove on the midline just anterior to the branchiostegal membranes. The

branchiostegal membranes are fused to one another across the mid-
line. In other ictalurids these membranes are free and the gular fold is
well developed. These features of *Trogloglanis* are unique, advanced
conditions within its family, but similar conditions can be found in
catfishes belonging to other families.

SENSE ORGANS.—*Trogloglanis* is similar to all other icta-
lurids in possessing four pairs of barbels: maxillary, nasal, inner and
outer mental (Figure 2). Each maxillary barbel arises from the edge of
the upper lip just above the mouth angle. They reach posteriorly to at
least the opercular bones, about 18% of the standard length.

Each nasal barbel is a prolongation of the anterior rim of the
posterior nostril. In length the nasal barbels approximate the maxil-
lary barbels. A single individual, SIOH-51-350-18A♀, has bifurcated
nasal barbels. This is a teratological condition that is occasionally
observed in other catfishes. The rim of the posterior nostril is not
otherwise elevated. The rim of the anterior nostril is expanded,
especially posterolaterally, to form a flattened or cup-like disc around
the nasal aperture.

The mental barbels arise from the skin covering the mandible
behind the sensory canal and pores (Figure 2). The outer pair are
slightly longer than the inner pair (ca. 14.5% and 13.7% of the
standard length), but all reach to about the edge of the branchiostegal
membrane.

Compared to other members of its family *Trogloglanis* has a
relatively short maxillary barbels and long nasal barbels. These
features are quite variable within epigean species and no clear trends
in barbel length evolution are seen.

There is no external trace of eyes in *Trogloglanis*, but the orbits
are demarcated by the infraorbital sensory canals (Figures 2, 6) and
lateral spines on the sphenotic bones lying subcutaneously just
behind the orbits (Figure 6). Eyes have been completely lost in the
other two cave-dwelling ictalurids: *Satan eurystomus* and *Prietella
phreatophila*. There is some variability in eye size among surface
living ictalurids within and between species. Interestingly, some
surface populations of the brown bullhead, *Ictalurus nebulosus*,
exhibit polymorphism in eye development from complete absence to
normal (Weisel and McLaurey, 1964; see also Hubbs and Bailey, 1947,
p. 12). Phyletic eye absence is obviously a derived condition within
catfishes, but it would seem to have minimal systematic significance.
Parallel loss of eyes among cave dwelling creatures is a well known
fact. Among ictalurids too, where *Satan* and *Prietella* are clearly the
sister groups of *Pylodictis* and *Noturus* respectively, eye loss has
occurred in parallel. Thus, the absence of eyes is not evidence for close
relationship among these troglogbites.

The head sensory canal system of *Trogloglanis* (Figure 2) is
basically similar to that of the generalized siluriform pattern as

described by Taylor (1969, p. 11-14, Pl. 1) and Lundberg (1970, 1975b). Posteriorly, the temporal canal has two pores between the supracleithrum and temporal region. The rear one is just above the point of attachment of the opercular membrane, the other is slightly more anterior. All living ictalurids possess these temporal canal pores.

The supraorbital canal normally has five pores in ictalurids (Taylor, 1969; Lundberg, 1970), whereas many other catfish groups have six. In *Trogloglanis* the posteriormost supraorbital pore is near the junction of the supraorbital and infraorbital canals in the frontal bone. This corresponds to the parietal branch pore of the supraorbital canal (Lundberg, 1975b, Figure 1B). The parietal branch is not prolonged caudally in *Trogloglanis* as it is in other ictalurids and many other catfishes. The short condition appears to be derived. The next anterior pore is above the orbit. *Trogloglanis* matches other North American and many other catfishes in having this open toward the dorsal midline.

The three anterior pores of the supraorbital canal are associated with the nasal bone (Taylor, 1969). Running forward in *Trogloglanis* these are: posteromedially adjacent to the posterior nostril, midway between the nostrils, and anteromedially adjacent to the anterior nostril. This arrangement is like that of all other ictalurids, except *Pylodictis* and *Satan* which have the anterior pore displaced forward, and a few species of *Noturus* and *Prietella* which have the second pore fused with the anterior pore of the infraorbital canal. These last two conditions are advanced; *Trogloglanis* has thus retained a primitive configuration of anterior supraorbital pores.

In *Trogloglanis*, as in other ictalurids, the infraorbital canal branches off from the supraorbital in the frontal bone. Most non-ictalurids have this bifurcation in the sphenotic bone. The forward shift of this sensory canal bifurcation is related to invasion of the skull roof by jaw musculature (Lundberg, 1970, 1975b). Eight, more or less equally spaced pores are associated with the infraorbital canal in *Trogloglanis*. Taylor (1969) reported seven infraorbital pores in one specimen. The anterior infraorbital pore (L1 of Taylor, 1969) is immediately posterior to the anterior nostril. Taylor noted that ictalurids usually possess seven pores, except *Trogloglanis* and *Prietella* in which there are usually eight. In *Prietella* the extra pore seems to be due to an interruption of the posterior part of the canal and both ends come to the surface. In *Trogloglanis* the canal is complete so it appears that a pore has been added to the canal. Both of these conditions are advanced among ictalurids, but they are independent of one another.

The preoperculomandibular canal of *Trogloglanis* has modally 10 pores. There are three counts of 11 pores in ten bilateral counts made. Suttkus (1961) reports right and left counts of ten pores on his

fish. Six or seven pores are associated with the mandibular part of the canal. The canal is complete in *Trogloglanis,* and the anteriomost pores are widely separated on either side of the mandibular symphysis. Taylor (1969) has documented considerable taxonomic variation in the preoperculomandibular canal among ictalurids. *Trogloglanis* appears to have retained the primitive condition of the canal. The modal count of 10 pores is a feature shared with *Ictalurus* and some species of *Noturus.* Many species of *Noturus* and *Prietella* have 11 pores modally. Reminiscent of its infraorbital canal, the extra preoperculomandibular pore in *Prietella* is due to an interruption in the upper part of the canal. *Pylodictis* and *Satan* have increased the number of pores to 12. In cases of increased pore number, except for *Prietella,* pores are added to the mandibular part of the canal; the number of pores in the preopercular part is always four or five. Furthermore, *Pylodictis* and *Satan* share an additional advanced condition of this canal in having the anterior end of each side open to a median symphyseal pit or a single common pore.

The lateral line canal of *Trogloglanis* joins the temporal canal over, or in, the supracleithrum as in other ictalurids. The canal runs over the horizontal skeletagenous septum and terminates at the level of the anterior part of the adipose fin (Figure 1). The canal is at first subcutaneous but caudally it breaks up into segments which become progressively shorter and raised above the level of the general integument as small keels. The last few segments lack pores and the central lumen. This keel-like structure of the lateral line canal is unique to *Trogloglanis* among ictalurids and this is clearly a derived condition. Morphogenetically it must result from a failure of the posterior lateralis placodes to sink into the skin. In surface living ictalurids as well as most other catfishes the lateral line canal is buried in the skin and complete, or nearly so. Within the family, besides *Trogloglanis,* the canal is markedly incomplete in *Satan* and *Prietella.* In both of these troglobites the terminus of the canal lies anterior to the adipose fin. Although shortening of the canal is an advanced condition, it is one that seems to have developed in parallel among the cave catfishes.

In addition to the lateralis system two other kinds of putatively sensory structures are present on the body of *Trogloglanis.* Hubbs and Bailey (1947) referred to these with the descriptive terms "fine" and "coarse cilia". The "fine cilia" are slender, tapering structures, averaging about .3mm in length. Posterior to the occiput they are generally distributed over the integument. Structures similar to these "fine cilia", but much shorter, are found in other ictalurids. The "coarse cilia" are unique to *Trogloglanis* among ictalurids, but Poulson (1963, Figure 4C) illustrates similar "tactile" receptors in *Amblyopsis spelaea.* In the catfish these are sparsely distributed dorsolaterally from the occiput to the flanks near the adipose fin. The

"coarse cilia" are about equal in length to the fine variety, but they are much stouter and usually swollen at their tips. Nothing is known of the functions of these structures. Accessory or hypertrophied mechanoreceptors and chemoreceptors or even electroreceptors might evolve in relation to sightless life in interstitial waters.

FINS.—The dorsal fin of *Trogloglanis* is high and has a nearly straight margin, whereas most ictalurids have a more rounded dorsal fin margin. The fin is supported by an inverted V-shaped spinelet, defensive spine, and six or seven soft rays (Figure 1,32B). The defensive spine is long and robust. It is devoid of ornamentation on all sides. The first few soft rays are prolonged beyond the spine tip. A stout defensive spine is present in all ictalurids (Figures 35B,D,F,H) except *Prietella*, in which it is weakly ossified and segmented at the tip. *Prietella* also has lost the spinelet. These features of spine reduction in the Mexican blindcat are uniquely derived within the family. Except for excessive spine length (see p. 00), and perhaps the fin shape, *Trogloglanis* has a primitive dorsal fin structure.

Trogloglanis has a large adipose fin (Figure 1): in length it is roughly one-third that of the standard length, and it is slightly higher than the depth of caudal peduncle musculature (well preserved only in SIOH51-379-18A). Although there is a distinct posterior flap on the fin, it is adnate to the back and narrowly connected to the upper part of the caudal fin by a ridge of ray-less integument. Hubbs and Bailey (1947) reported that the adipose fin was separated from the procurrent caudal rays in UMMZ 190921 but this individual is not as well preserved as the Scripps specimen.

There are three basic varieties of the adipose fin encountered among ictalurids. The species of *Ictalurus* and *Pylodictis* have a short to moderately long fin that is high, free from a smoothly rounded back and free from the caudal fin. At the other extreme, *Prietella* and many species of *Noturus* have a long, low adipose fin which is adnate to the back and caudal fin. The condition of the adipose fin in *Trogloglanis* is intermediate, and it is also seen in *Satan* and a number of species of *Noturus* (especially in the subgenus *Rabida*). Most other catfishes, and other teleosts which have the fin, possess a free adipose fin as adults. Therefore, the adnate conditions are regarded as derived. Taylor (1969, p. 217) believed the opposite, stating that the adnate adipose is a retention of the "primitive finfolds". This is more likely a paedomorphic retention of an embryonic condition common to nearly all catfishes, not a phyletically primitive condition.

Trogloglanis has a rounded anal fin which contains 16 or 17 fin rays (Figure 32). The fin shape is similar to that of other ictalurids with the exception of *Ictalurus furcatus* which has a much straighter margin. Comparison of anal fin ray counts is given in Table 4 in which species are chosen to show the extremes within their groups.

TABLE 4

MODES AND RANGES OF ANAL FIN RAY COUNTS IN 17 SPECIES OF ICTALURIDS
SELECTED TO SHOW VARIABILITY OF GENERA AND SUBGENERA. WITHIN EACH
POLYTYPIC HIGHER TAXON THE SPECIES ARE CHOSEN TO ILLUSTRATE THE MINIMUM,
CENTROID AND MAXIMUM FIN RAY COUNT. DATA ARE SUMMARIZED
FROM TAYLOR (1969) AND LUNDBERG (1970).

	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	Sample Size
Trogloglanis pattersoni						—	X																					5
Ictalurus																												
(*Ictalurus*) *mexicanus*										—	X	—																13
(*Ictalurus*) *punctatus*														—	—	—	—	X	—	—	—							154
(*Ictalurus*) *furcatus*																		—	—	—	—	—	—	—	X	—	—	32
(*Amiurus*) *brunneus*						—	—	—	X	—																		107
(*Amiurus*) *nebulosus*										—	X	—	—	—														51
(*Amiurus*) *natalis*														—	—	—	X	—	—									34
Noturus																												
(*Noturus*) *flavus*			—	—	X	—	—																					132
(*Schilbeodes*) *gyrinus*	—	—	—	X	—	—																						310
(*Schilbeodes*) *insignis*			—	—	—	—	X	—																				141
(*Schilbeodes*) *funebris*									—	—	X	—	—	—	—	—	—											170
(*Rabida*) *munitus*	—	X	—	—																								147
(*Rabida*) *miurus*		—	—	X	—	—																						197
(*Rabida*) *elegans*			—	—	X	—	—	—																				111
Prietella phraeatophila	—	—	X	—																								13
Pylodictis olivaris				—	—	X	—																					36
Satan eurystomus								—	X																			3

Trogloglanis falls toward the low end of the range for the Ictaluridae. A literature survey of several families indicates that the most common anal ray counts among catfishes fall between 16 and 20. On this basis *Trogloglanis* may be suspected of having a relatively primitive count within its family.

The shape of the caudal fin is well preserved in one specimen (SIOH 51-379-18A) where it is slightly emarginate (Figure 1). In this feature *Trogloglanis* is most similar to *Pylodictis*, *Satan* and the bullheads (subgenus *Amiurus*) with exception of *Ictalurus catus*. *I. catus*, all species of the subgenus *Ictalurus*, *Astephus* and *Hypsidoris* possess a distinctly lobed tail, probably the primitive condition for the family. The most advanced tail shape character states are in *Noturus* where there is variation from truncate to definitely rounded tails.

Trogloglanis has 8 upper and 9 lower principal caudal fin rays. This is the primitive count for most catfishes (Lundberg and Baskin, 1969). Also, there are 11–14 upper and 10–16 lower procurrent caudal rays. Taylor (1969) presents data on procurrent caudal rays for *Noturus*, but other genera remain to be studied in regard to this feature. All that can be said now is that, assuming a primitive 8 + 9 principal ray count, *Noturus*, not *Trogloglanis*, is characterized by a high number of procurrent caudal rays and this is a derived condition relative to other ictalurids. *Trogloglanis* does not appear to be unusual in caudal ray counts.

The pectoral fin of *Trogloglanis* is supported by a long, sharp spine (Figure 4) and 8 or modally 9 soft rays. The anterior edge of the spine is smooth. The posterior edge bears a series of nearly evenly spaced, and usually unicuspid dentations. Distally the dentations are erect to slightly retrorse; proximally they become antrorse. Also, the most proximal dentations are attached to the dorsal half of the spine shaft.

Within the Ictaluridae and throughout the Siluriformes the most common pectoral soft ray count is 9, and this is assumed to be the primitive count. Some ictalurids such as *Ictaluris natalis* and several species of *Noturus* show a trend toward lower counts of 7 and 8. And, some have modal counts of 10 (*Ictalurus brunneus*, *I. pricei*, *I. furcatus*, *Noturus flavus*, *Satan eurystomus*, *Astephus antiquus*) or 11 (*Ictalurus balsanus*, *Pylodictis olivaris*). Thus, there has been divergence in the pectoral ray count within the family, but this has not involved *Trogloglanis*.

Relative to the other troglobites, *Trogloglanis* has long, remarkably well ornamented pectoral spines (Figures 4,5). The uniform spacing and robust development of the posterior spine dentations are not advanced features since these conditions are quite common in surface living catfishes. The dorsal attachment of the proximal dentations on the spine shaft is a departure from the ancestral

bilateral symmetry of the spine, an organ derived from a single fin ray (Figures 4, 5). Among ictalurids a comparable dorsal shift of dentations is found uniformly in the subgenera *Amiurus* (*Ictalurus*) and *Schilbeodes* (*Noturus*), *Pylodictis*, and *Satan*.

There is no axillary pore above the base of the pectoral spine in *Trogloglanis*. This pore is usually present in *Noturus* but variable in other members of the family, frequently being lost with growth.

The rounded pelvic fins of *Trogloglanis* are supported by 8 (modally) or 9 soft rays (Figures 1, 40). The outer ray is simple and a pelvic splint is lacking. Many other ictalurids have modal counts of 8 pelvic rays too. Taylor (1969) reported modal counts of 9 for several species of *Noturus*. *Astephus* has 9 pelvic rays. Also, in *Pylodictis* and *Satan* 10-rayed individuals are common. Throughout the Siluriformes pelvic ray counts of 6 are most common, and departures from this are believed to be derived. The lowest modal pelvic ray count in the family is 7 in *Hypsidoris* and this is taken as primitive for the family. The count of 8 is relatively primitive among the living taxa. The absence of the pelvic splint is an advanced feature but one that has occurred many times among catfishes. *Trogloglanis* shares this loss character with *Prietella* and *Noturus*.

VENT.—In males of *Trogloglanis* the anus is located immediately in front of a transverse depression. The urogenital papilla, with a single terminal aperture, is a small mound of tissue situated in the depression. In females the urinary and reproductive tracts have separate openings. The oviducts have a common broad aperture just behind the anus. The urinary ducts lead to a urinary papilla which is larger in size than that of the male. I can find no clear taxonomic differences in external urogenital organs of either sex among ictalurids.

OSTEOLOGY

NEUROCRANIUM.—Nearly the entire bony skeleton of *Trogloglanis*, but especially the skull, is weakly ossified (Figures 6, 7). All bones of the head are thin, and large areas of the braincase and suspensorium remain cartilaginous or membranous. The skull roof lacks bony ornamentation; crests, processes and fossae for muscle attachment are generally weakly developed.

Throughout the genera *Ictalurus* (Figures 8–11), *Pylodictis* (Figures 18, 19B), *Astephus* and *Hypsidoris* the adult skeleton is well ossified, points of muscle attachment are sharply defined, and dermal bones subjacent to the skin bear various types of ornamentation (tubercles, ridges, grooves, pits). In contrast, ictalurids which do not attain a large adult body size, say less than 100mm SL, have weakly formed bony skeletons like *Trogloglanis*. This group includes many species of *Noturus* (Figures 15, 16, 17A, 19A), *Satan* and *Prietella*
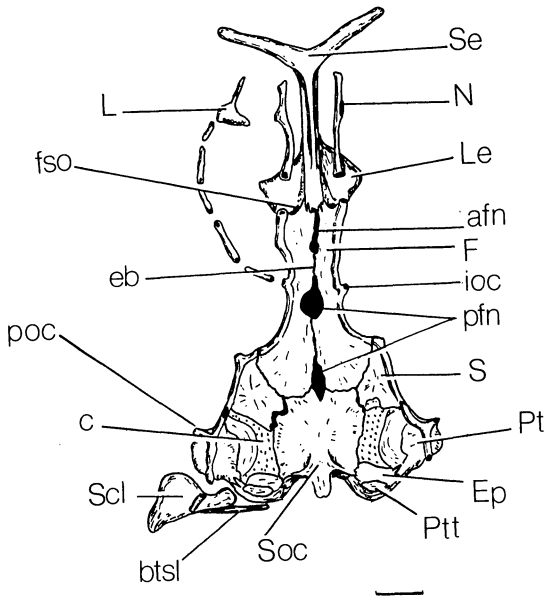
Fig. 6. Skull in dorsal view of *Trogloglanis pattersoni*. Scale 2mm. For abbreviations see text (Materials and Methods).

(Figure 17B). The poorly ossified skeletons of these small fish appear to be paedomorphic. At the same time, skeletal reduction in *Trogloglanis* may be directly adaptive to likely depauperate energy resources in a deep subterranean habitat and/or correlated reduction of locomotory and feeding activity. A parallelism in skeletal reduction is suggested between *Trogloglanis* and deep sea fishes of the abyssal zone. Sam Sweet (pers. comm.) informs me, however, of his observations that the skeletons of troglobitic amblyopsid fishes and plethodontid salamanders are as well ossified as their closest epigean relatives.

The neurocranium of *Trogloglanis* (Figure 6), disregarding the cornua of the supraethmoid and the nasals, has the form of an isosceles triangle, with its sides tapering sharply toward the snout. In all other ictalurids (Figures 8–15) the anterior part of the skull is much broader, giving a more rectangular shape. The skull form of *Trogloglanis* appears to be a uniquely derived condition within the family.

The pattern of cranial bones in *Trogloglanis* is shared with other ictalurids and most other catfishes (Figures 6–19).

The Y-shaped supraethmoid is the most extreme in the family in having a narrow neck and divergent cornua (Figures 6, 7). The supraethmoid neck, joining the bone to the skull, has a dorsal median ridge that lies just beneath the skin. The cornua are delicate and lack medially directed processes, thus leaving a broad and shallow median
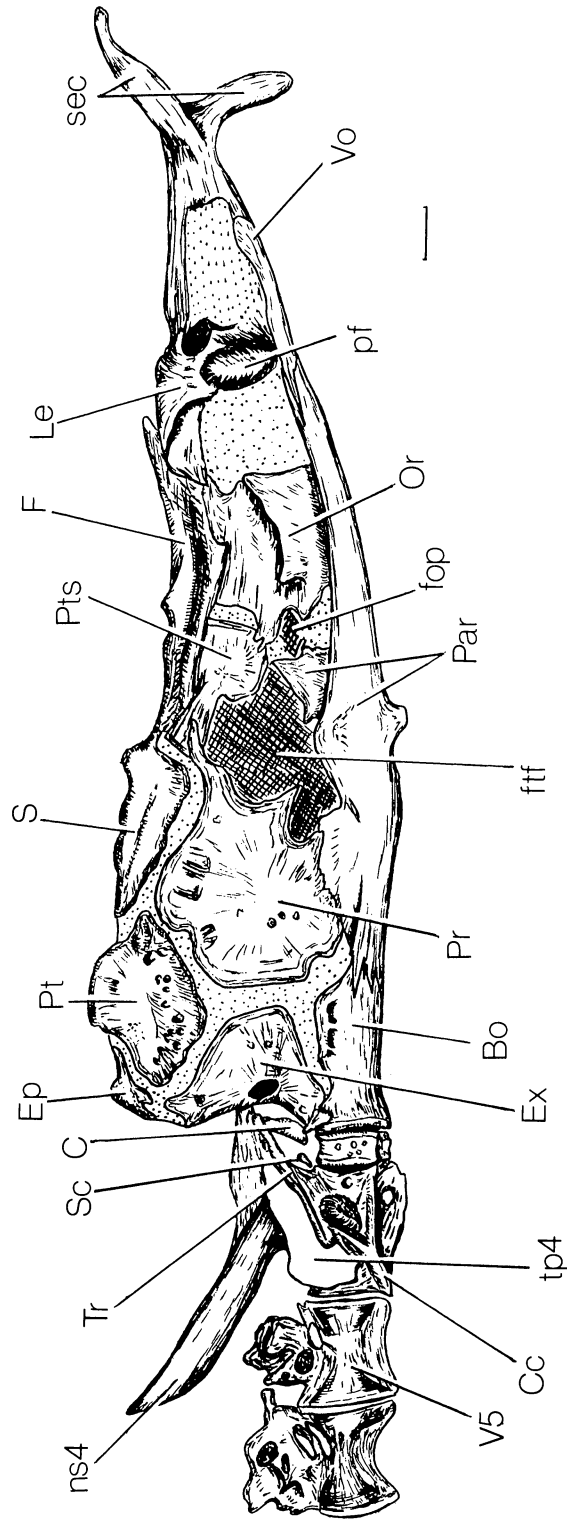
Fig. 7. Skull and anterior vertebrae in ventrolateral view of *Trogloglanis pattersoni*. Scale 1mm. For abbreviations see text (Materials and Methods).

Fig. 8. Skull of *Ictalurus (Ictalurus) furcatus*, UMMZ 169031-S-1. A. Dorsal view. B. Ventral view. Scale 5mm. For abbreviations see text (Materials and Methods).

Fig. 9. Skull of *Ictalurus* (*Ictalurus*) *punctatus*, UMMZ 186274-S-1. A. Dorsal view, with right nasal bone illustrated to the side. B. Ventral view. Scale 5mm. For abbreviations see text (Materials and Methods).
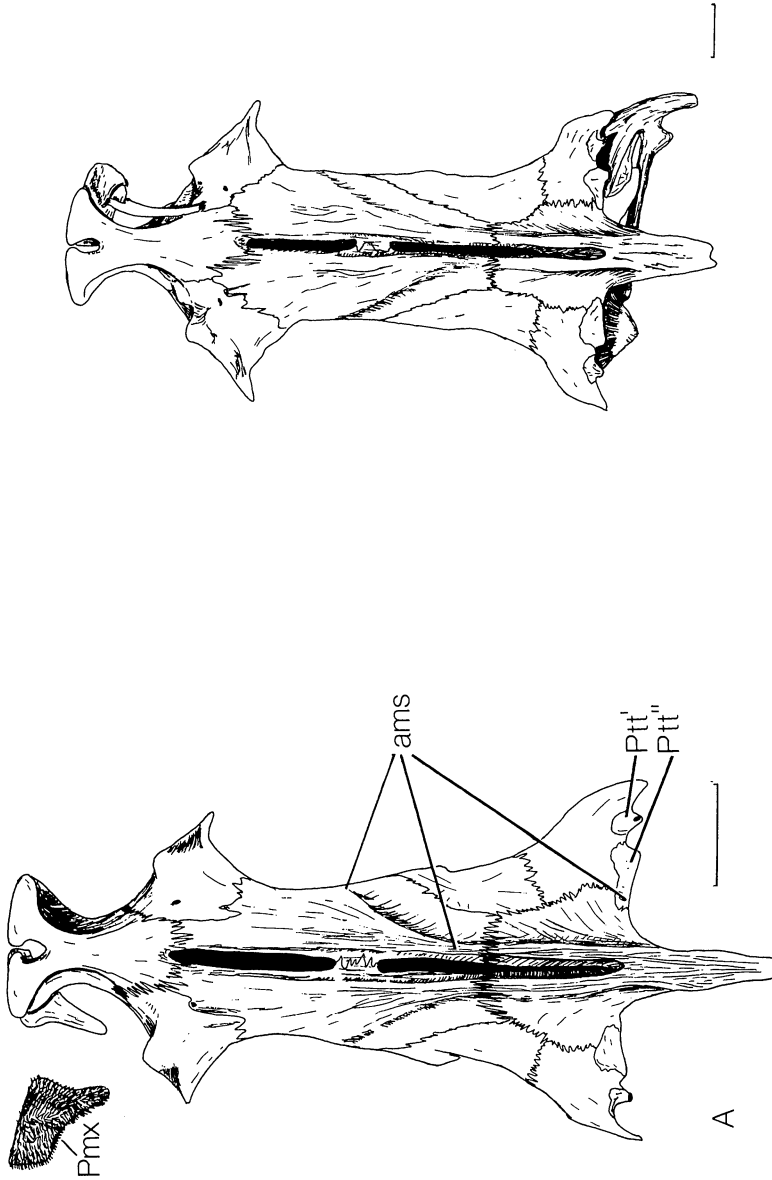
Fig. 10. Skulls in dorsal view. A. *Ictalurus (Ictalurus) balsanus*, UMMZ 169854-S-1; left premaxilla illustrated in ventral view to the side. B. *Ictalurus (Ictalurus) lupus*, UMMZ 186503-S-1. Scales 5mm. For abbreviations see text (Materials and Methods).
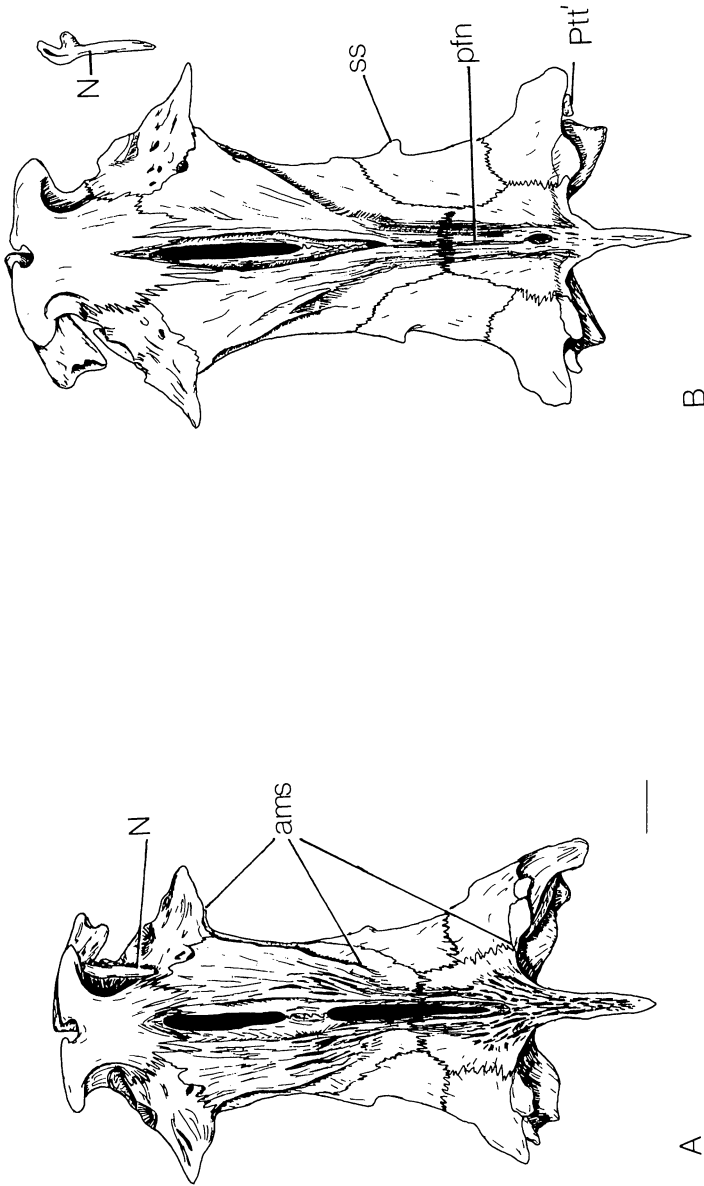
Fig. 11. Skulls in dorsal view. A. *Ictalurus (Amiurus) catus*, UMMZ 186240-S-2. B. *Ictalurus (Amiurus) brunneus*, UMMZ 186241-S-9, right nasal bone illustrated to the side. Scale 5mm. For abbreviations see text (Materials and Methods).
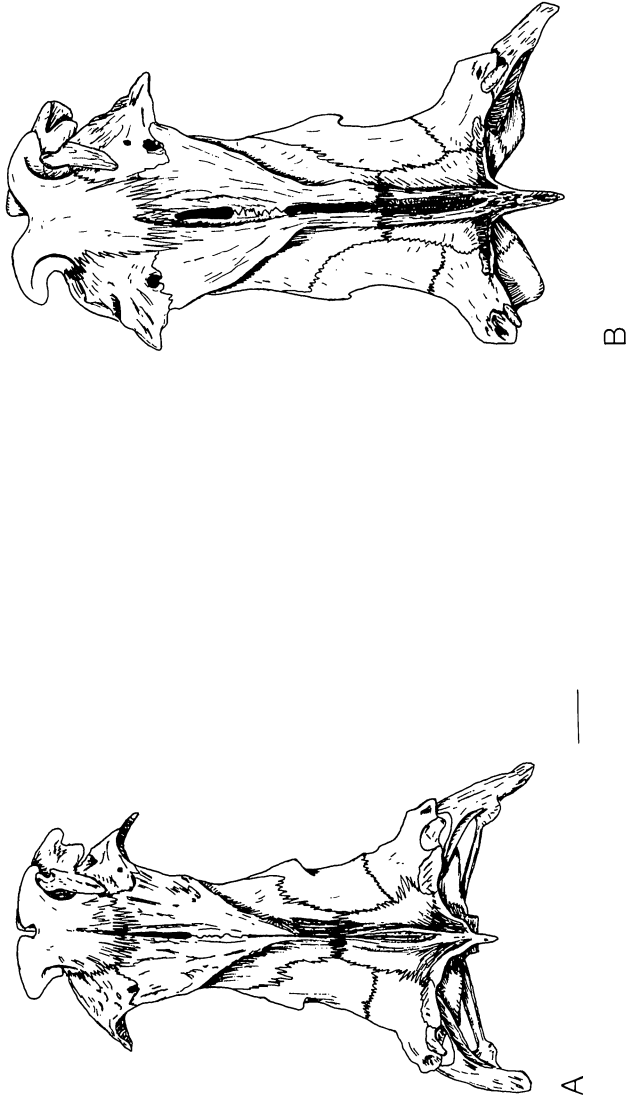
Fig. 12. Skulls in dorsal view. A. *Ictalurus (Amiurus) natalis*, UMMZ 171788-S. B. *Ictalurus (Amiurus) melas*, UMMZ 169035-S-17. Scale 5mm.
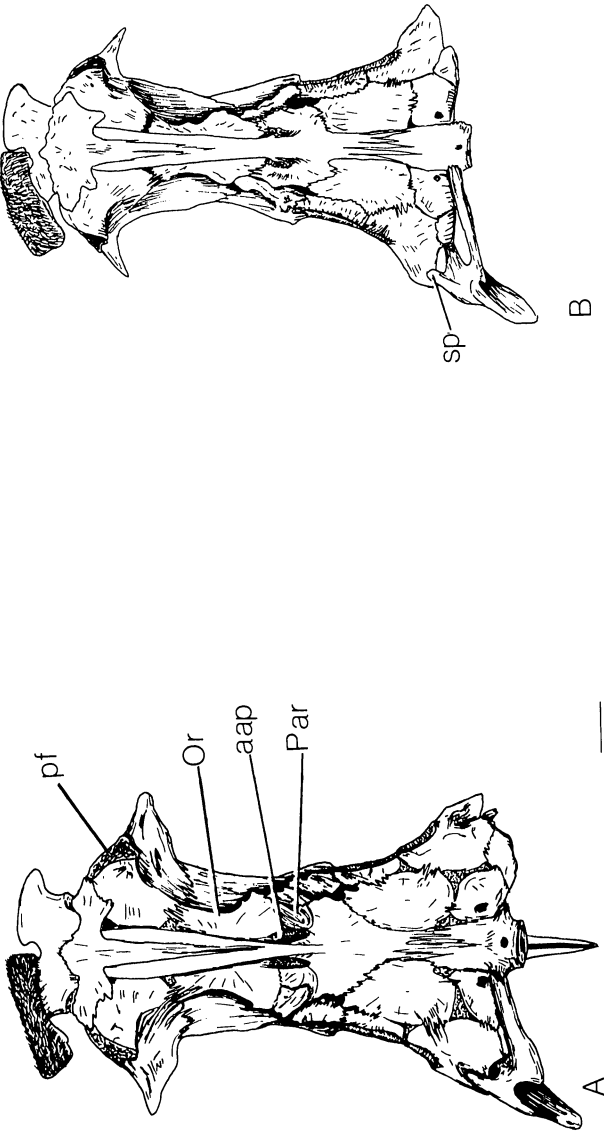
Fig. 13. Skulls in ventral view. A. *Ictalurus (Amiurus) catus*, UMMZ 186240-S-2. B. *Ictalurus (Amiurus) natalis*, UMMZ 171788-S. Scale 5mm. For abbreviations see text (Materials and Methods).
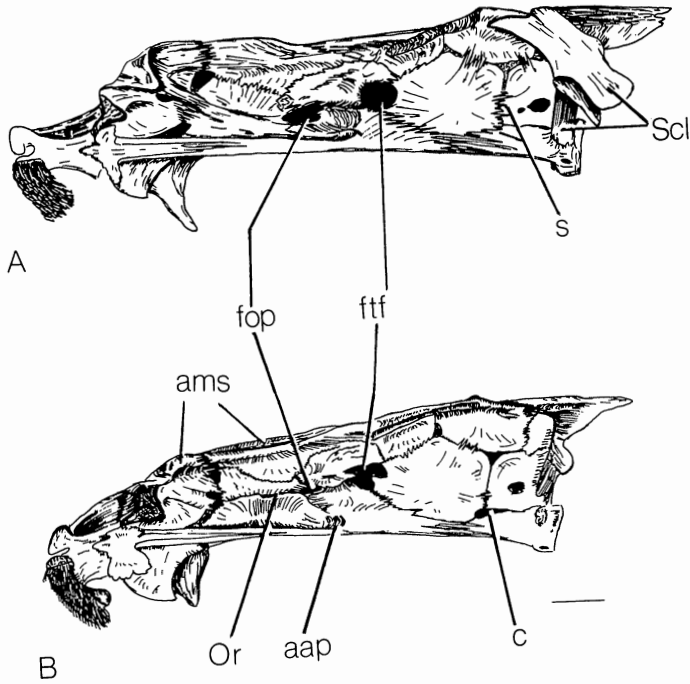
Fig. 14. Skulls in ventrolateral view. A. *Ictalurus (Ictalurus) punctatus*, UMMZ 186274-S-1. B. *Ictalurus (Amiurus) catus*, UMMZ 186240-S-2. Scale 5mm. For abbreviations see text (Materials and Methods).

cleft. No other ictalurid has a supraethmoid as slender as *Trogloglanis*. Of all ictalurids the extinct *Hypsidoris* comes closest to *Trogloglanis* in this character. Several ictalurids, however, have widely divergent cornua lacking mesial processes: *Pylodictis* (Figure 18), *Satan*, some species of *Noturus, Ictalurus melas* (Figure 12B) and the fossil species in the genera *Astephus* and *Hypsidoris*. Because of the widespread distribution of this form of the cornua among catfishes outside of the Ictaluridae it is regarded here as primitive. Most species of *Ictalurus, Noturus* and *Prietella* have narrow median clefts and mesial processes on the supraethmoid cornua and various catfishes in other families have a similar condition. This is a derived form of the supraethmoid but it certainly has been developed, and perhaps lost again, independently within siluriforms a number of times.

Each slender nasal bone in *Trogloglanis* is pierced by three foramina for the supraorbital sensory canal (Figure 6). These same foramina are present throughout the Siluriformes. The main part of the canal passes through the anterior and posterior foramina. The intermediate foramen, located anterolaterally about one third of the way along the length of the bone, is for the tube which leads to the
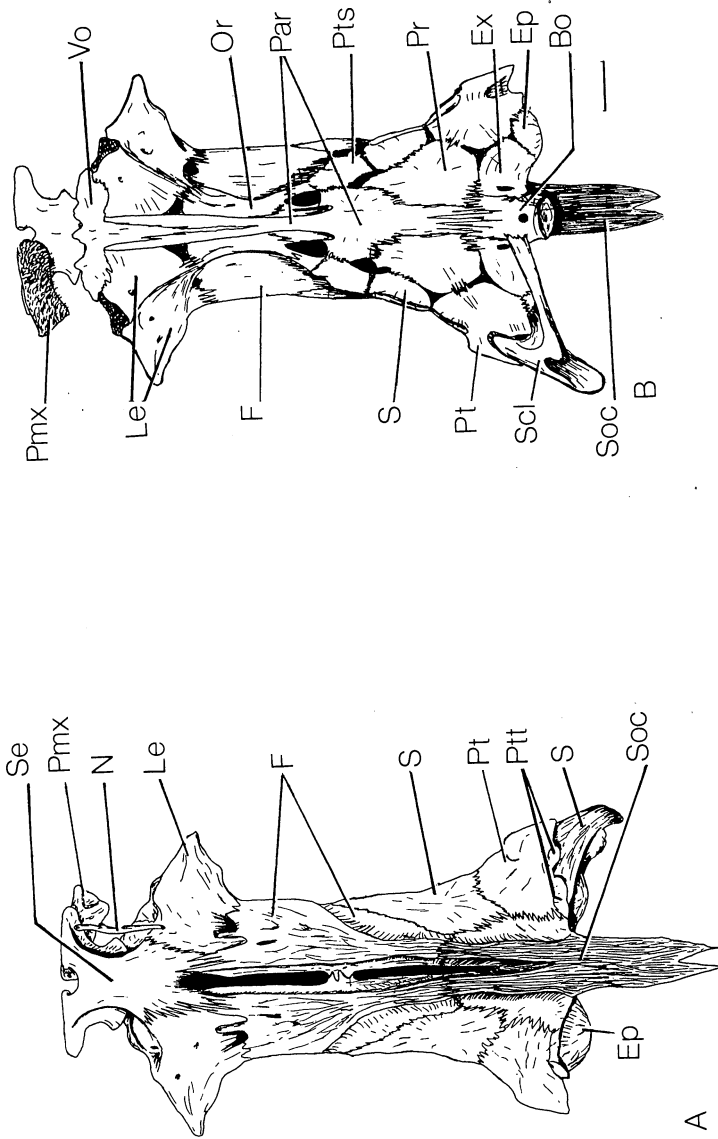
Fig. 15. Skull of *Noturus (Noturus) flavus*, UMMZ 126365-S. A. Dorsal view. B. Ventral view. Scale 5mm. For abbreviations see text (Materials and Methods).
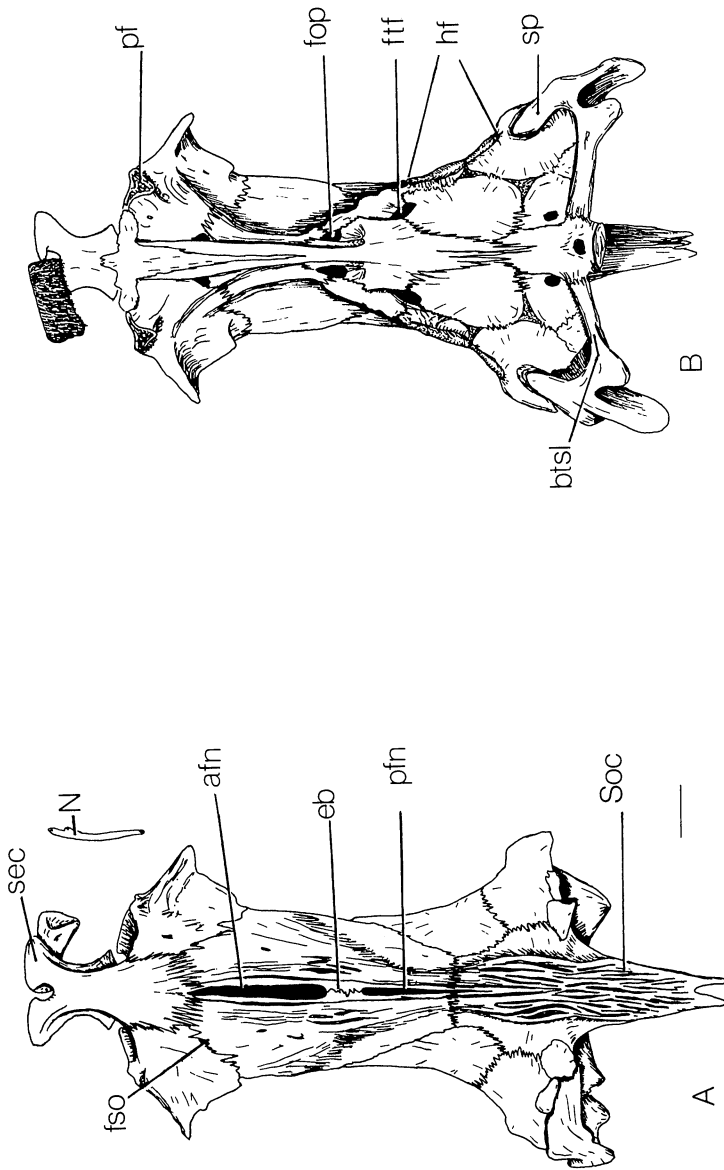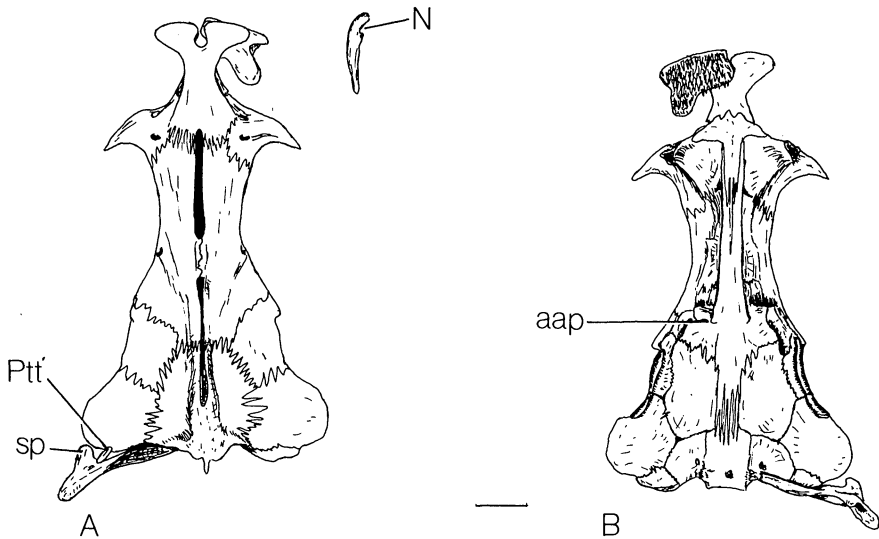
Fig. 16. Skull of *Noturus (Rabida) stigmosus*, UMMZ 165841-S-1. A. Dorsal view, with right nasal bone illustrated on the side. B. Ventral view. Scale 2.5mm. For abbreviations see text (Materials and Methods).

second supraorbital pore (N2 of Taylor, 1969). In having a slender nasal *Trogloglanis* is like members of the subgenus *Ictalurus* (Figures 8–10) and many catfishes outside of the family. The other living ictalurids have an inflated nasal bone which sometimes becomes flattened and heavily ossified (Figures 11, 12, 15, 18). These latter conditions appear to be derived within the family.

The lateral ethmoid bones are more weakly developed in *Troglogloglanis* than in any other catfish examined (Figures 6, 7). In siluriform fishes this element generally appears to have a compound origin from endochondral and perichondral ossification of the antorbital process plus a dorsal, usually ornamented dermal component. In *Trogloglanis* there is, however, no indication of a dermal component. Also, ossification of the antorbital process is incomplete, with the facet for the palatine bone remaining cartilaginous. This uniquely derived condition of the lateral ethmoid in *Trogloglanis* may be paedomorphic.

The frontal bones, the largest elements in the skull roof of *Trogloglanis* (Figure 6), lack crests for muscle attachment on the dorsal surface. The superficial ophthalmic foramen between the frontal and lateral ethmoid is not enlarged as it is in some ictalurids (Figures 8A,9A). The supraorbital sensory canal is enclosed along the lateral edge of the frontal bone. In addition to its rear and forward terminal openings, there are three foramina for side branches of this canal in the frontal. Of these three the most posterior foramen is laterally directed, midway along the bone. This leads to the infra-
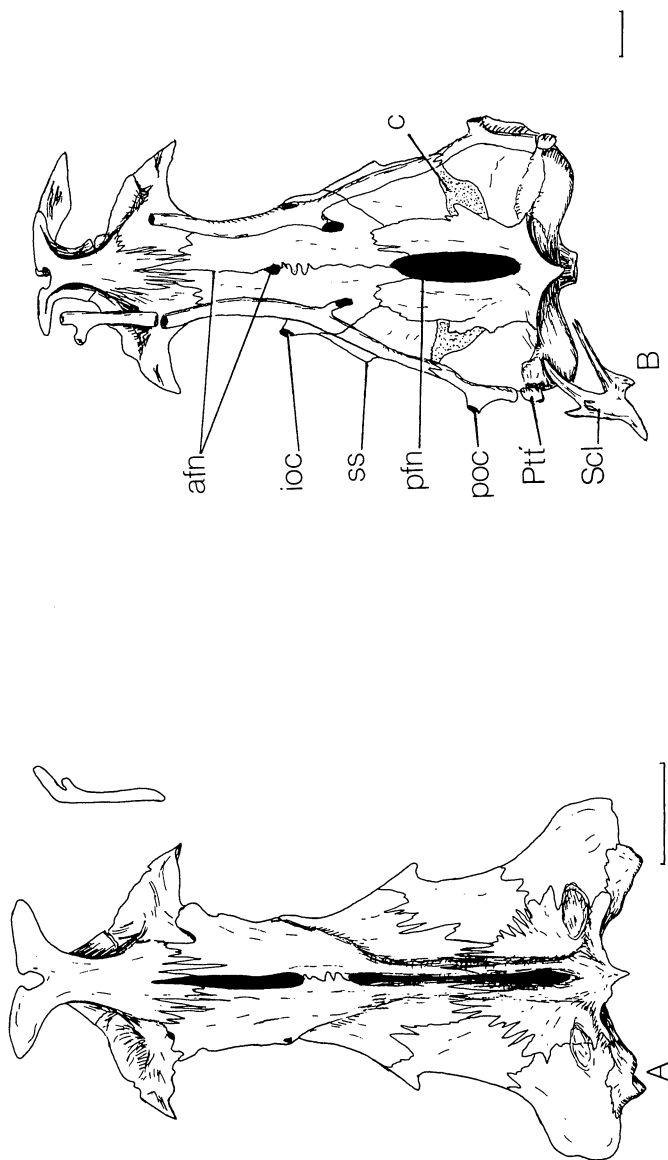
Fig. 17. Skulls in dorsal view. A. *(Noturus (Schilbeodes) insignis*, UMMZ 186551-S-1, with right nasal bone illustrated to the side, scale 5mm. B. *Prietella phreatophila*, UMMZ 173788, scale 1.5mm. For abbreviations see text (Materials and Methods).
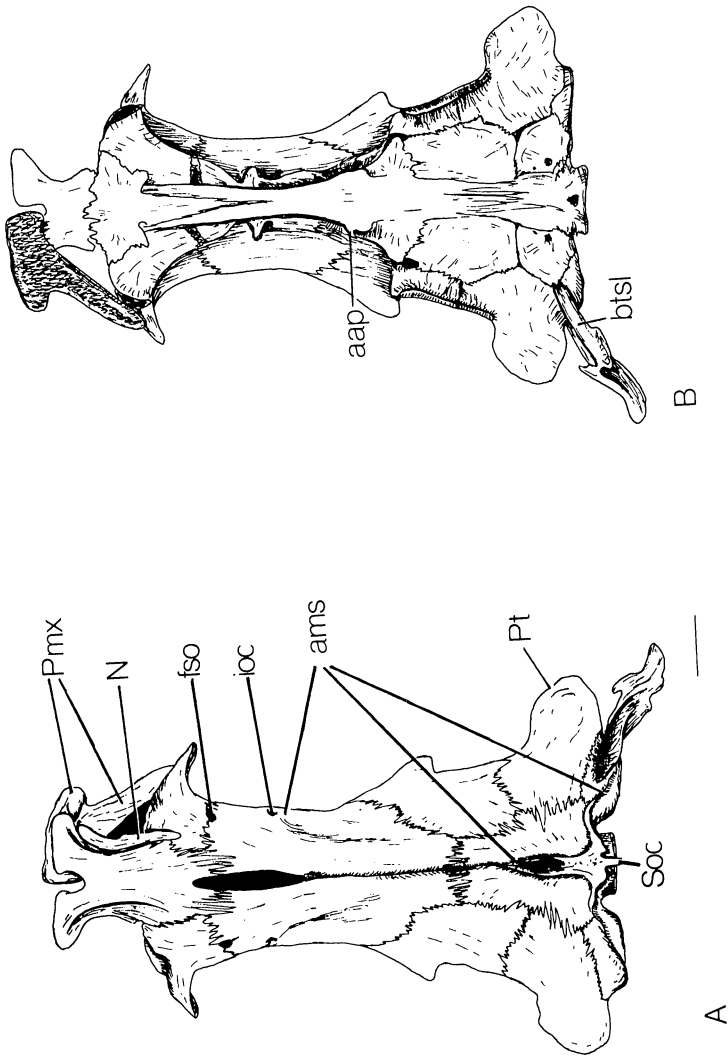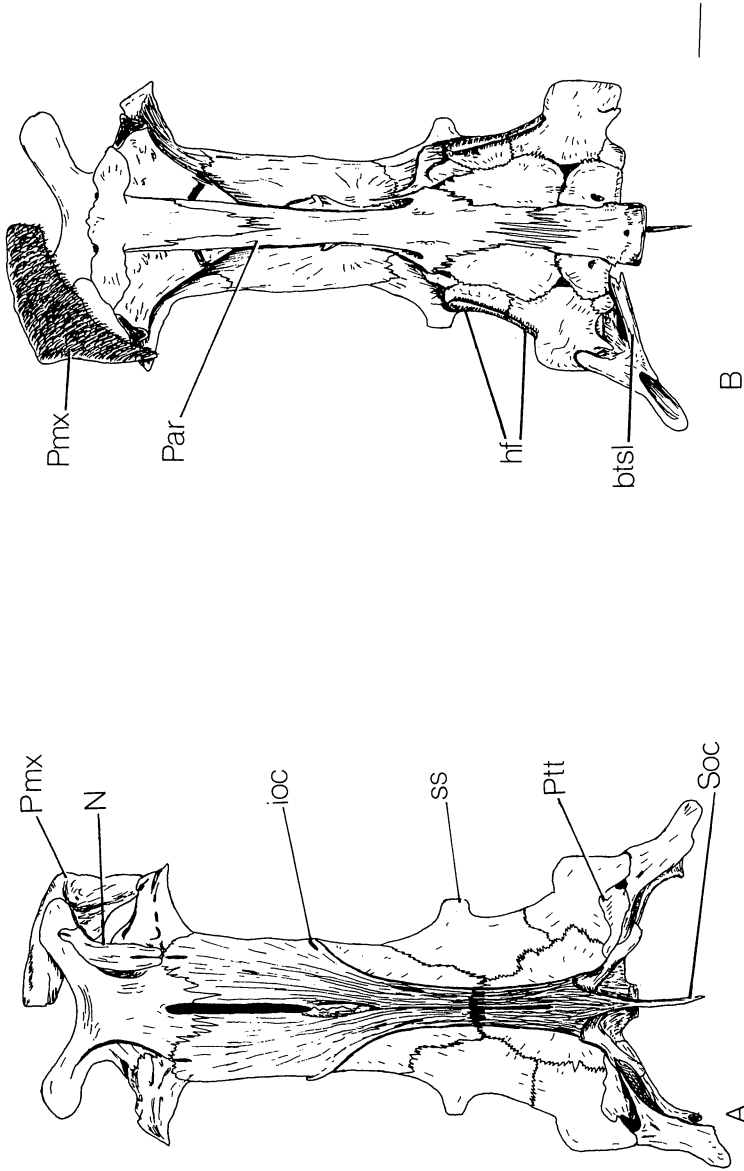
Fig. 18. Skull of *Pylodictis olivaris*, UMMZ 169029-S-1. A. Dorsal view. B. Ventral view. Scale 5mm. For abbreviations see text (Materials and Methods).
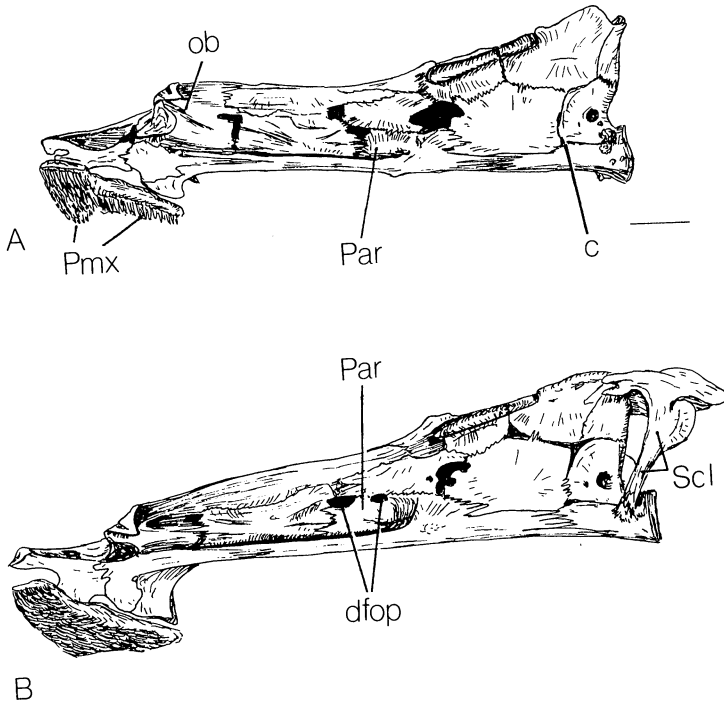
Fig. 19. Skulls in ventrolateral view. A. *Noturus (Noturus) flavus*, UMMZ 126365-S. B. *Pylodictis olivaris*, UMMZ 169029-S-1. Scale 5mm. For abbreviations see text (Materials and Methods).

orbital canal. The middle and anterior foramina open toward the midline to the parietal branch and the orbital branch in that order. This arrangement is the same as that found in other living members of the family. The extinct ictalurid genera *Astephus* and *Hypsidoris*, as well as most other living catfishes have the infraorbital canal emerging from the sphenotic bone, or at the frontal-sphenotic suture. The anterior displacement of the point of branching into the frontal in modern ictalurids, and a few other catfishes such as *Diplomystes* (Diplomystidae), *Brachyglanis* (Pimelodidae) and some *Liocassis* (Bagridae), is associated with jaw muscle invasion of the skull roof. This is a derived condition within the order, but one which has evolved in parallel a few times. *Trogloglanis* has much reduced head musculature; no fibers of the adductor mandibulae are found over the skull roof, nor are there prominent ridges or crests present on the skull roofing bones for muscle origin. That this is a secondary reduction of musculature in *Trogloglanis* is strongly suggested by the frontal location of the infraorbital branch bifurcation.

The epiphyseal bar joins the frontals to one another anterior to the level of the infraorbital canal bifurcation in *Trogloglanis* (Figure 6) and other ictalurids. In front of the bar, the anterior cranial fontanelle is open. The fontanelle does not extend forward onto the

supraethmoid bone as it does in most other catfishes. This may be due to the extreme narrowing of the supraethmoid noted above. The shape of the anterior fontanelle is relatively uniform among ictalurids, but in *Prietella* (Figure 17B) the frontals suture weakly on the midline almost completely, thus occluding the fontanelle. In back of the epiphyseal bar *Trogloglanis* has an open, but irregularly shaped posterior cranial fontanelle. Other ictalurids have variously constricted posterior fontanelles, with more definite margins (Figures 8–12, 15–18). The odd form of this fontanelle in *Trogloglanis* appears to be derived.

The supraoccipital of *Trogloglanis* is a large, roughly square bone (Figure 6). Its separation from the pterotics by large blocks of cartilage is exceptional. Other ictalurid catfishes have at least some sutural contact of these bones. This is another derived, paedomorphic feature of *Trogloglanis*.

The posteriorly directed supraoccipital spine is broad and moderately produced. It does not contact the supraneural at the dorsal fin base. The surface of the spine and the main part of the bone lack dermal ornamentation and crests for muscle attachment. Considerable systematic variation of the supraoccipital spine exists among ictalurids (Figures 8–12, 15–18). The primitive condition for living ictalurids appears to be a broad and long spine with contact being made, or nearly so, with the supraneural. This gives support to the dorsal spine locking mechanism. Except for the subgenus *Ictalurus*, living ictalurids have a smaller supraoccipital spine in width and/or length. *Trogloglanis* appears to have a moderately advanced condition here: broad, like *Ictalurus*, but short, like *Amiurus*.

The supraoccipital spine was primitively ornamented all over its dorsal surface with coarse grooves, pits and ridges (Lundberg 1970, 1975a). In most living ictalurids the ornamentation is restricted to the top of a "sagittal" crest which marks the medial limit of jaw musculature. In *Trogloglanis*, as a consequence of weak ossification and musculature, there is neither ornamentation nor "sagittal" crest.

The sphenotic bone of *Trogloglanis* is similar to that found in other ictalurids except that the supraorbital canal is embedded at its margin (Figures 6, 7). Sphenotic contacts are entirely synchondral with the pterotic, pterosphenoid and prootic, reflecting the weakly ossified nature of the head skeleton and are probably derived phyletically within the family. In *Pylodictis* the sphenotic bears a large, angular spine on the anterolateral margin (Figure 18). In the subgenus *Ictalurus* the sphenotic spine is minute or absent (Figures 8–10). In other members of the family, including *Trogloglanis*, this process is moderately developed, and rounded or pointed (Figures 6, 7, 11, 12, 15–17). This last condition is closest to that found in the majority of catfishes outside of the family and to extinct genera, and therefore it appears primitive among living species.

The sphenotic does not reach anterior to the level of the

epiphyseal bar in *Trogloglanis, Pylodictis, Prietella* and *Noturus* among ictalurids. In *Ictalurus, Astephus, Hypsidoris* and many other catfishes the tip of the sphenotic bone reaches further forward. The former condition thus appears to be derived.

The pterotic bone of *Trogloglanis* is weakly ossified, with only synchondral contacts being made with surrounding neurocranial bones (Figures 6, 7). This likely paedomorphic characteristic is derived within the family. The temporal sensory canal bifurcates with the pterotic to form the supraorbital canal and the preoperculo-mandibular canal. The latter exits laterally from the bone as it does in other ictalurids.

Although originally part of the shoulder girdle, the posttemporal bone has become an integral part of the skull roof in catfishes (Lundberg, 1975b). This bone tends toward reduction in several lineages of catfishes. I reported three conditions of this bone in ictalurids. *Trogloglanis* presents a fourth, uniquely derived state— the bone is represented by a small dermal plate lying between the pterotic and supraoccipital, above the epioccipital (Figure 6), and the laterosensory part of the bone has been lost. *Noturus* and *Prietella* present the opposite condition in having retained only the latero-sensory part of the posttemporal (Figures 16, 17). In *Ictalurus* both of these small bones are present but separate (Figures 8–12). *Pylodictis* and the extinct genera appear to have retained the most primitive condition in having both bones united as a single compound element (Figure 18).

The epioccipital bone (Patterson, 1975) does not exhibit notable taxonomic variation among ictalurids. In *Trogloglanis* it has the standard relations to the surrounding supraoccipital, posttemporal, pterotic, and exoccipital (Figure 7). The exoccipital also has the basic character of that bone in other ictalurids (Figure 7). Only syn-chondral contracts are made with the supraoccipital, epioccipital, pterotic and prootic, but at its posteroventral corner a suture is made with the basioccipital. Other ictalurids have sutures between the exoccipital and its dorsal neighbors (Figures 8, 9, 13–16, 19). Exoc-cipital contact with the prootic is variable, however, *Noturus* (Figures 16, 19A) and *Prietella* lack exoccipital-prootic sutures like *Trog-loglanis*. Other ictalurids have sutures here (Figures 8B, 9B, 13, 14, 19B). Unlike the synarthroses of the dermal skull roof, joints between the deep endochondral bones of the otic capsule are synchondal in many catfish groups and other ostariophysans. Provisionally then the absence of sutures is regarded as primitive for ictalurids but the correlation between body size and development of sutures again suggests paedomorphosis in *Trogloglanis*.

The basioccipital in *Trogloglanis* (Figure 7) is strongly sutured with the parasphenoid and has a well developed attachment surface for the transscapular ligament. There is, however, no sutural contact

between the basioccipital and prootic. This last feature is regarded as primitive. It is shared with all living ictalurids except members of the subgenus *Ictalurus* (Figures 8, 9, 14A) which have a strong superficial suture between these bones.

The prootic is the largest element in the side wall of the braincase in *Trogloglanis* (Figure 7). Its synchondral contacts with the otic capsule bones have been noted. This bone has a long union with the parasphenoid which is sutural anteriorly. A slender process runs forward from the prootic to make a short suture with the ptero-sphenoid above the trigeminofacial foramen. Among ictalurids this contact is variable, being fairly extensive in *Pylodictis* (Figure 19B), but reduced or absent in others (Figures 8, 9, 13, 14, 19A). In most catfishes the contact between the prootic and pterosphenoid is short, and this is thought to be primitive.

The parasphenoid of *Trogloglanis,* and of catfishes generally, extends along the floor of the braincase from the supraethmoid to the basioccipital (Figure 7). Its relations to surrounding bones are not extraordinary except for that with the pterosphenoid. Catfishes, including all ictalurids except *Trogloglanis,* usually have a well developed ascending wing on the parasphenoid which sutures with the pterosphenoid, thereby separating the trigeminofacialis and optic foramina (Figures 8, 9, 13, 14, 19). *Diplomystes,* and at least some trichomycterids (Baskin, pers. comm.) also lack this bony wing. In *Trogloglanis* the parasphenoid tapers toward the pterosphenoid and fails to make contact with it. This results from failure in para-sphenoid ossification of the membrane anterior to the trigemino-facialis foramen. The remaining foramen appears enormous and the bony wing is weak, representing another derived feature of *Trogloglanis.*

The pterosphenoid of *Trogloglanis* is similar to that of other ictalurids except as noted above. The orbitosphenoid has the typical trough-shaped form (Figure 7). Horizontal shelves on this bone extend laterally just beyond the edges of the parasphenoid stem. There is much variability in ictalurids in the degree of development of orbitosphenoid shelves. Members of the subgenus *Amiurus* have extremely broad shelves (Figures 13, 14B), and most other species have them narrow or obsolescent (Figures 8, 9, 14A, 15B, 16, 18B, 19). *Trogloglanis* has an intermediate condition. The extreme conditions are probably derived since many non-ictalurids have some develop-ment of the shelves.

In spite of the absence of eyes, the optic foramen is well developed in *Trogloglanis* (Figure 7). An optic nerve is not visible in the alizarin stained specimen, whereas the trigeminal and facial nerves are. I suspect that the whole optic stalk is aborted in *Trog-loglanis* (see below).

In *Trogloglanis* the vomer has lost the characteristic T-shape

found in most other catfishes (Figure 7 cf. Figures 8, 9, 13, 14, 16, 18B, 19). It has, instead, an elongate teardrop form, a condition uniquely derived among ictalurids.

INFRAORBITALS.—The infraorbital bones in *Trogloglanis* consist of five simple tubular ossicles plus the lacrimal (first infra-orbital) (Figure 6). These ossicles, as in other catfishes, surround the sensory canal between the branch points for the short tubes which lead to pores. The posteriormost ossicle is adjacent to the point of exit of its sensory canal from the frontal. The lacrimal has a central plate with medial and anterior processes. The arrangement of the infra-orbital bones is basically that found in other ictalurids and many other catfish groups. The primitive number of infraorbitals within catfishes is five, assuming that the dermosphenotic has fused with the autosphenotic. This assumption is based on the observations that the upper end of the infraorbital canal is embedded in the sphenotic in most catfishes, and the dorsal surface of the bone is usually orna-mented with dermal bony tubercles or ridges. An increase in the number of elements has occurred in several lineages, including the Ictaluridae. Among ictalurids the lowest and primitive number of bones is six (*Prietella*, *Trogloglanis*). The species of the subgenus *Ictalurus* vary with six or seven infraorbitals (Figure 20). *Amiurus* (Figure 20B), *Noturus* and *Pylodictis* have modally seven bones. The number of infraorbitals in the extinct ictalurids is unknown.

SPLANCHNOCRANIUM.—In *Trogloglanis* (Figure 21), as in most catfishes (Figure 24), the maxillae and palatines are excluded from the functional upper jaw and these bones are modified to support and move the maxillary barbels. Each maxilla is a splint of bone which tapers into the base of its barbel. Proximally there are dorsal and ventral condyles for articulation with the palatine. Except for its delicate construction the maxilla of *Trogloglanis* is not essentially different from those of other ictalurids.

The palatine bone of *Trogloglanis* (Figures 21A,B) is rod-like, with cartilaginous tips and a condyle for movable articulation with the lateral ethmoid. It has an unusual shape, being elongated and
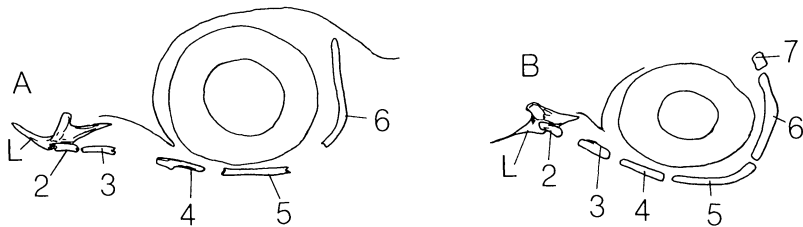
Fig. 20. Infraorbital bones. A. *Ictalurus (Ictalurus) mexicanus*, UMMZ 164713. B. *Ictalurus (Amiurus) catus*, UMMZ 155198.
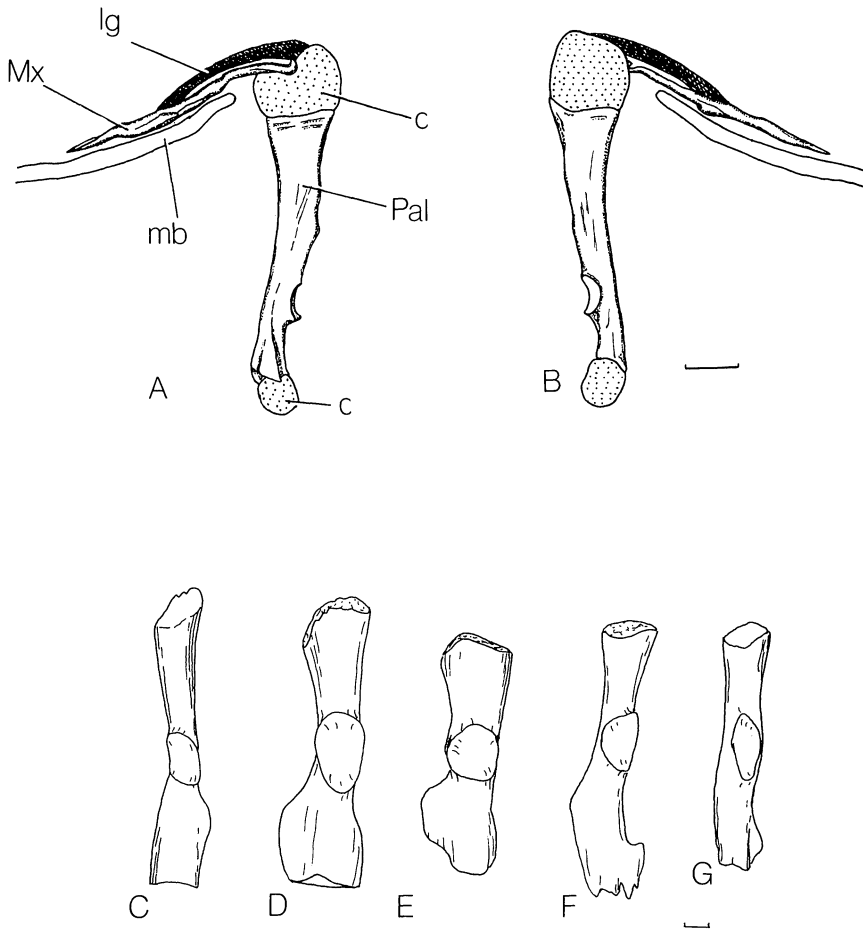
Fig. 21. Palatine and maxilla of *Trogloglanis pattersoni*. A. Dorsal view. B. Ventral view. Palatine bones in medial view, C. *Ictalurus (Ictalurus) punctaus*, UMMZ 186239-S-3; D. *Ictalurus (Amiurus) catus*, UMMZ 186249-S-2; E. *Ictalurus (Amiurus) nebulosus*, UMMZ 182047-S-1; F. *Noturus (Noturus) flavus*, UMMZ 126365-S-1; G. *Pylodictis olivaris*, UMMZ 169029-S-1. Scales 1mm. For abbreviations see text (Materials and Methods).

somewhat swollen anterior to its lateral ethmoid condyle. In other ictalurids (Figures 21C–G), as in most other catfishes, the palatine is approximately equally developed on either side of the condyle. The lopsided form of this bone in *Trogloglanis* is a uniquely derived one.

The premaxillae are the functional elements of the biting upper jaw in catfishes (Figures 8–19). These bones are highly specialized in *Trogloglanis* (Figure 22C): toothless and reduced to perforated, paper-thin sheets of bone. The bone is more or less quadrangular and dorsolaterally each has a low crest for articulation with the supra-ethmoid.

The mandible of *Trogloglanis* is also specialized, and as dis-
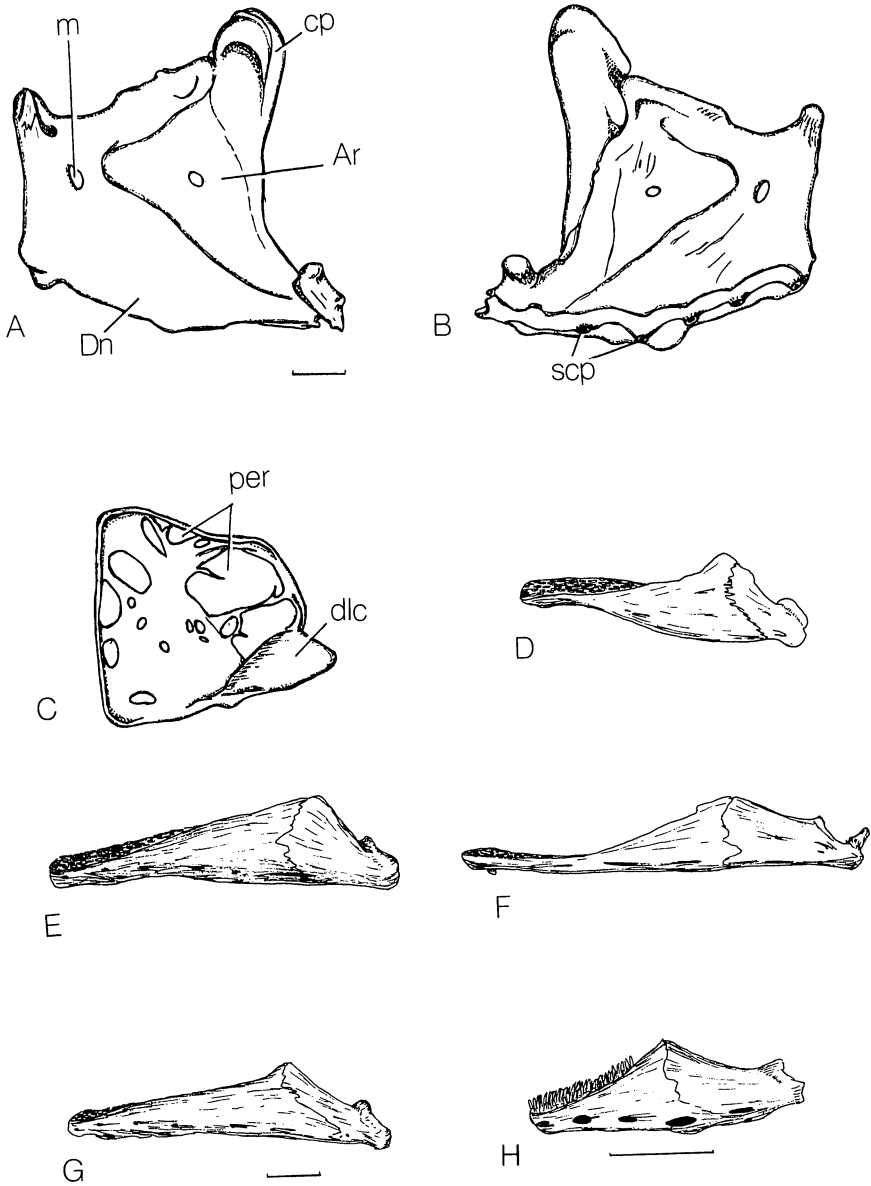
Fig. 22. Right side lower jaw skeleton of *Trogloglanis pattersoni*, A. Internal view, B. External view. C. Dorsal view of right premaxilla of *Trogloglanis pattersoni*. Scale for A, B and C 1mm. Left side lateral views of lower jaw skeletons, D. *Ictalurus (Ictalurus) lupus*, UMMZ 186503-S-1; E. *Ictalurus (Amiurus) brunneus*, UMMZ 186241-S-9; F. *Pylodictis olivaris*, UMMZ 169029-S-1; G. *Noturus (Noturus) flavus*, UMMZ 126365-S-1; H. *Prietella phreatophila*, UMMZ 173788. Scale for D–G 5mm, scale for H 1mm. For abbreviations see text (Materials and Methods).
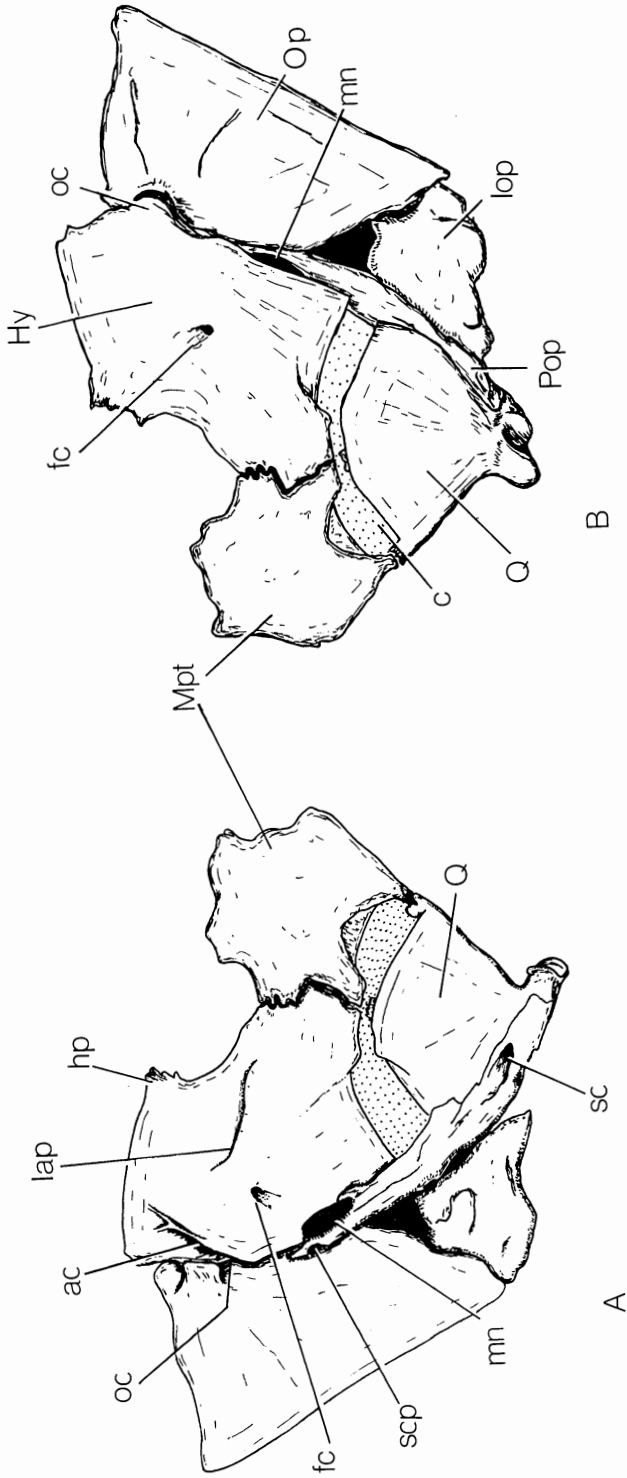
Fig. 23. Suspensorium and operculum of *Trogloglanis pattersoni*. A. Lateral view. B. Medial view. Scale 1mm. For abbreviations see text (Materials and Methods).
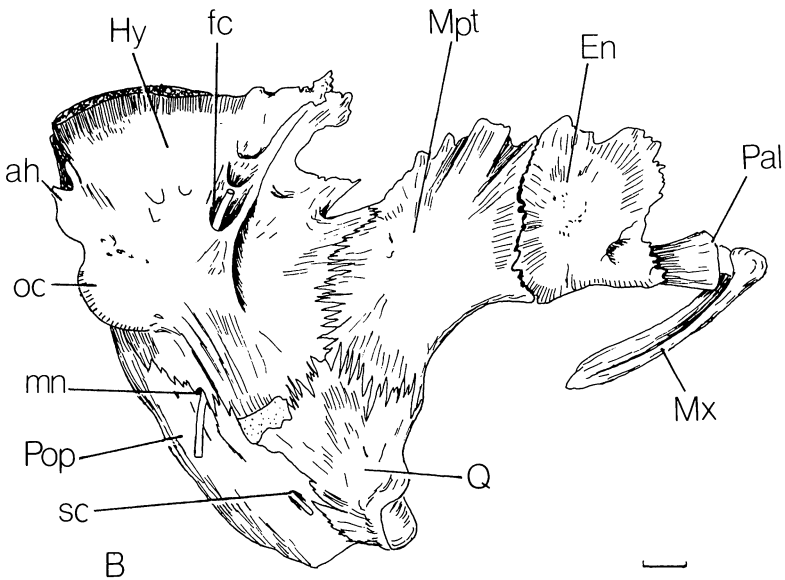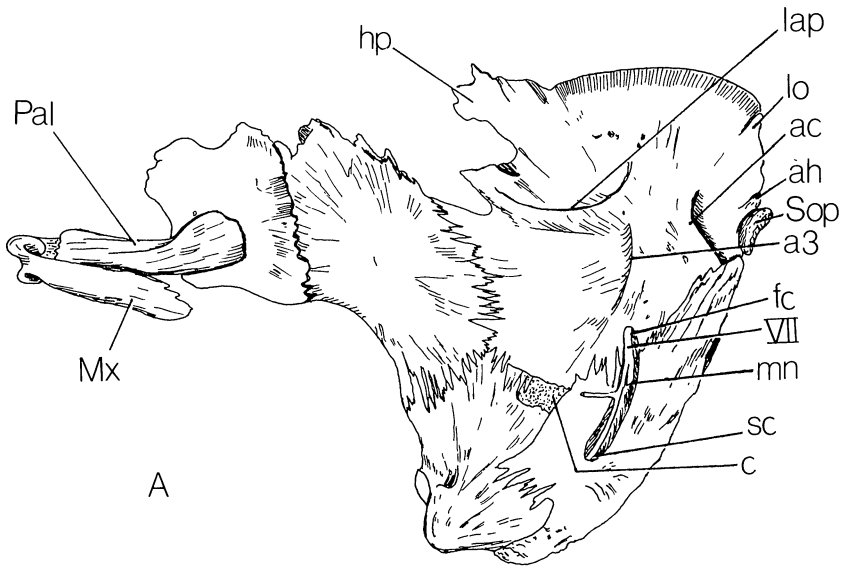
Fig. 24. Suspensorium, palatine and maxilla of *Ictalurus (Amiurus) serracanthus*, UMMZ 186258-S-4. A. Lateral view. B. Medial view. Scale 2mm. For abbreviations see text (Materials and Methods).
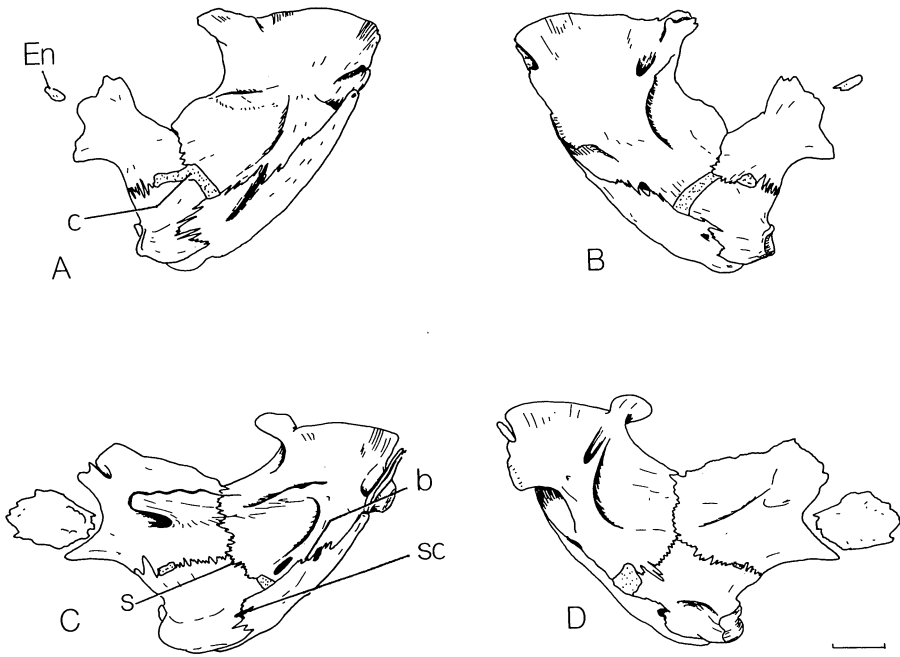
Fig. 25. Suspensoria. A. Lateral view of *Ictalurus (Ictalurus) punctatus*, UMMZ 186269-S-1.
B. Medial view of same. C. Lateral view of *Pylodictis olivaris*, UMMZ 169029-S-1. D. Medial
view of same. Scale 1mm. For abbreviations see text (Material and Methods).

tinctive in form as the premaxilla (Figures 22A,B). The articulated
mandibles are short and transversely oriented. Only the angular and
edentulous dentary bones can be discerned. The dentary is a deep and
thin blade. At the mandibular symphysis there are dorsal and ventral
articulating condyles. There is a single, centrally-placed mental
foramen. Five foramina lie along the lower edge for pores of the
mandibular canal. The angular bone is ventrally ossified where it is
firmly articulated, and conformable in shape with the dentary. The
articular facet is also well ossified. Uniquely, Meckel's cartilage is
produced dorsally to form a prominent unossified coronoid process.

The peculiar structure of the jaw elements of *Trogloglanis* sets
this fish apart from all other catfishes (cf. Figures 8–19, 22 D–H). The
overall shapes of the premaxillae and mandibles conform to the
fleshy lips which overlie the bones. The extreme foreshortening of the
mandibles is the structural basis for the permanently open mouth (see
above p. 00).

The suspensorium of *Trogloglanis* consists of hyomandibular,
preopercle, quadrate, and metapterygoid (Figure 23). The palatine,
described above, is functionally and anatomically separate from the
suspensorium. Neither endopterygoid nor ectopterygoid are present.
The ectopterygoid is absent in all ictalurids. The endopterygoid is

Fig. 26. Suspensoria. A. Lateral view of *Noturus* (*Schilbeodes*) *insignis*, UMMZ 147950-S-1. B. Medial view of same. C. Lateral view of *Prietella phreatophila*, UMMZ 173788. D. Medial view of same. Scale 1mm. For abbreviations see text (Materials and Methods).

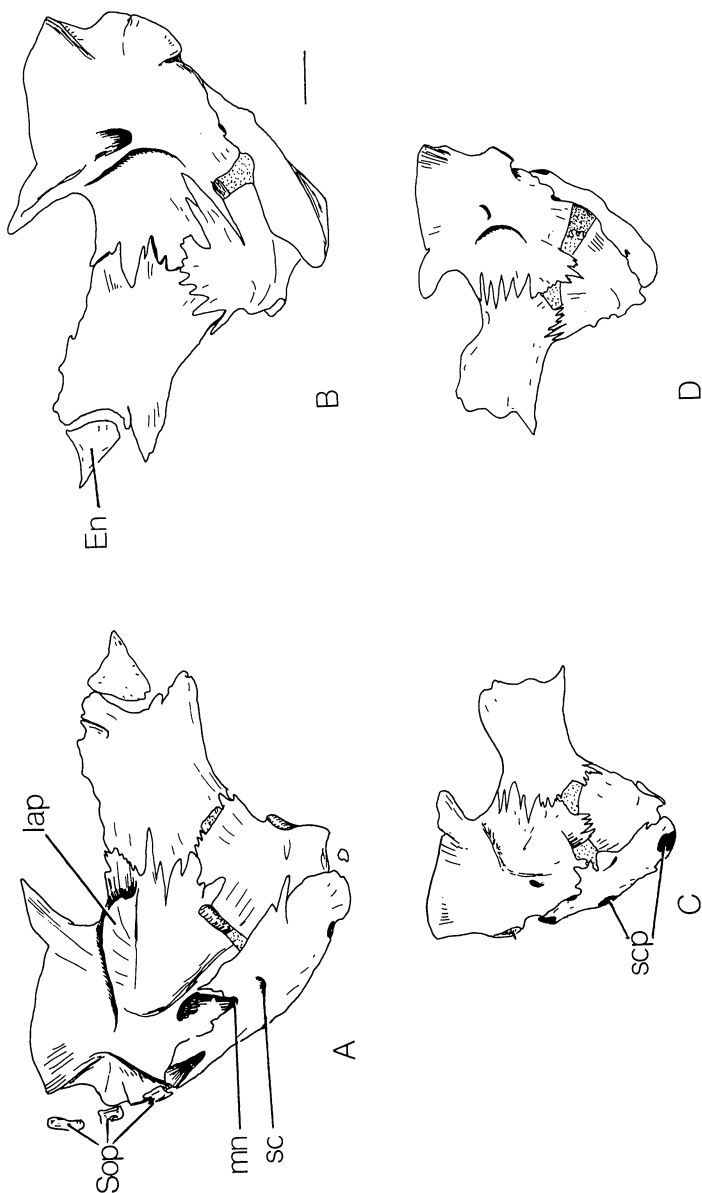usually present even if small (Figures 24–26). *Prietella* (Figure 26D) and some *Noturus*, like *Trogloglanis*, have lost this bone.

The metapterygoid is roughly pentagonal in form. It has synchondral and sutural contacts with the hyomandibular and quadrate. The synchondral contact is extensive like the primitive condition found in the subgenus *Ictalurus* (Figure 25A,B). The absence of sutures is believed primitive because sutures are lacking in many catfishes and other ostariophysans. The metapterygoid bone bears no distinctive ridges or crests for the attachment of muscles in *Trogloglanis*. This bone exhibits considerable variation in shape among ictalurid catfishes (Figures 24–26). That of *Trogloglanis* is peculiar in lacking a distinct anterior process from the ventral margin, and in having an irregular dorsal edge. Overall, this most resembles *Ictalurus melas* and *I. nebulosus*, and the absence of this anterior process is believed to be an advanced condition.

The quadrate of *Trogloglanis* has the triangular shape typical of most catfishes. As in the subgenus *Ictalurus* (Figure 25A,B) there is no sutural contact between the quadrate and hyomandibular. These appear to be primitive conditions. Among fossil catfishes *Astephus* has this suture, and *Hypsidoris* lacks it. Species of the subgenus *Amiurus, Noturus, Pylodictis* and even the diminutive *Prietella* have quadrate-hyomandibular sutures (Figures 24, 25G, 26).

The preopercle of *Trogloglanis* has a long contact with the hyomandibular broken by the mandibularis foramen for the ramus mandibularis of the facial nerve (Figure 23). The upper part of the preopercle has a tapered, tube-like process surrounding the preopercular sensory canal, with no suprapreopercle around the exposed part of the canal. Nowhere is the bone much expanded behind the sensory canal. Dorsally this bone terminates below the level of the opercular facet and adductor crest of the hyomandibular. The short preopercular upper limb of *Trogloglanis* resembles *Amiurus, Noturus, Prietella*, and *Pylodictis* (Figures 24, 25C, 26). Species of the subgenus *Ictalurus* (Figure 25A) and *Astephus* retain a more primitive condition in having the upper part of the preopercle extended above the level of the opercular facet and adductor crest. The lack of preopercular expansion for muscle origin in *Trogloglanis* may be a result of weakly developed head musculature. This lack of expansion and the suprapreopercle are conditions of *Prietella* also (Figure 26C).

The hyomandibular bone of *Trogloglanis* is a squarish element with a long cranial articulation on the sphenotic and pterotic (Figures 7, 23). The anterior process of the bone is short and evidently lacks contact with the pterosphenoid. The lack of articulation between these two bones is a primitive trait found also in *Noturus* and *Prietella. Trogloglanis* has two weakly developed muscle scars on the lateral face of the hyomandibular (Figure 23A). There is a centrally placed and horizontal levator arcus palatini crest which

serves as the insertion point for that muscle. An adductor crest runs obliquely across the posterodorsal corner of the bone toward a prominent opercular facet. This crest marks the separation between the dilitator operculi above and adductor mandibulae below. In *Ictalurus* (Figures 24, 25A) this adductor crest terminates at or above the opercular facet. This is a primitive state, shared with many other catfishes. *Trogloglanis* shares the advanced "low" position of this crest with *Noturus, Prietella* and *Pylodictis* (Figures 25C, D, 26). The weak expression of these crests in *Trogloglanis*, and the absence of several other hyomandibular characters, reflects the reduced head musculature. The hyomandibular features related to muscle attachment which are usually present in ictalurids but absent in *Trogloglanis* are: A_3 crest for the deepest layer of the adductor mandibulae, levator operculi crest, adductor hyomandibularis process, and adductor arcus palatini crest (Figure 24).

The outer foramen of the facial canal on the lateral face of the hyomandibular is distinctly separated from the mandibularis foramen in *Trogloglanis* (Figure 23A). In other living ictalurids, except *Noturus* and *Prietella*, the two foramina are adjacent or superimposed (Figures 24–26). The separated state is primitive and, since it is found in large extinct ictalurids (*Astephus*), it appears not to be a simple consequence of small body size.

The opercle and interopercle of *Trogloglanis* have a relatively primitive appearance (Figure 23). The opercle is broadly triangular and its dorsal edge is not truncated at the insertion of the levator operculi as in many ictalurids (Figures 27A–C). The interopercle is expanded posteroventrally as in the subgenus *Ictalurus* (Figures 28A–C) and many other catfish groups.

Following the orientation of the mandible, the long axis of the lower half of the hyoid arch (Figure 29F) is nearly transverse in *Trogloglanis*. The interhyal is a small bony nodule. The epihyal and ceratohyal are short and deep, and contact between them is primarily synchondral. Most likely this is a paedomorphic feature as nearly all catfishes have sutures between these bones (Figures 29A–D). The dorsal and ventral hypohyals are incomplete, caplike ossifications over their respective cartilages. The orientation of the hyoid arch and the shape of the ceratohyal are unique and advanced features.

Trogloglanis has ten branchiostegal rays articulating with the hyoid arch of each side. The inner two curve toward the midline and the lateral ones are flattened. Living ictalurids exhibit modal branchiostegal ray counts of eight to ten or eleven, except *Pylodictis* which has modally twelve rays. A high count is probably advanced and associated with the excessively broad and flattened head of this species (Lundberg, 1970). Branchiostegal ray counts in the extinct genera are uncertain, but there are at least 8 in *Astephus antiquus*.

The urohyal of *Trogloglanis*, like the isthmus, is broadly
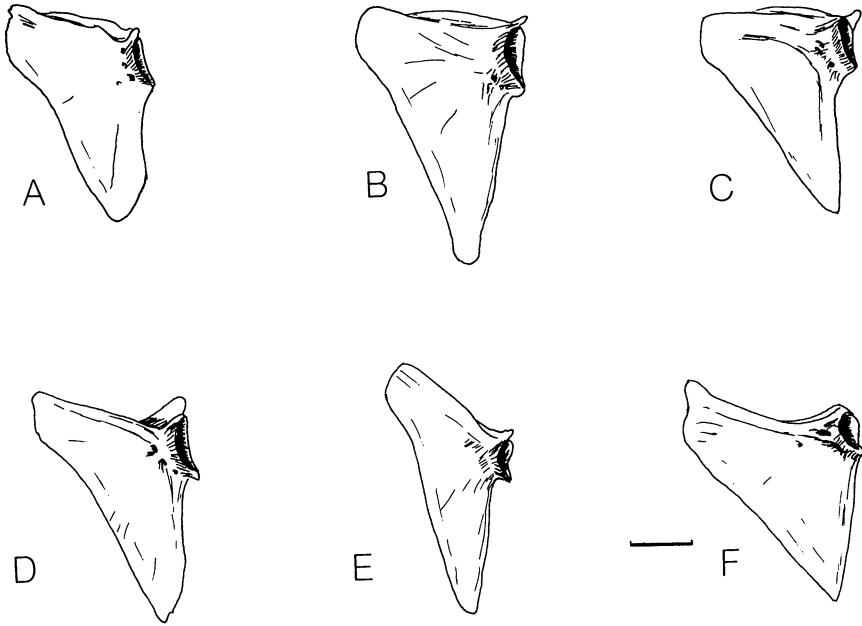
Fig. 27. Opercles in medial view. A. *Ictalurus (Ictalurus) furcatus*, UMMZ 169031-S-2. B. *Ictalurus (Amiurus) catus*, UMMZ 186249-S-2. C. *Ictalurus (Amiurus) nebulosus*, UMMZ 171787-S-1. D. *Ictalurus (Amiurus) brunneus*, UMMZ 186241-S-3. E. *Noturus (Noturus) flavus*, UMMZ 126365-S-1. F. *Pylodictis olivaris*, UMMZ 169029-S-1. Scale 5mm.
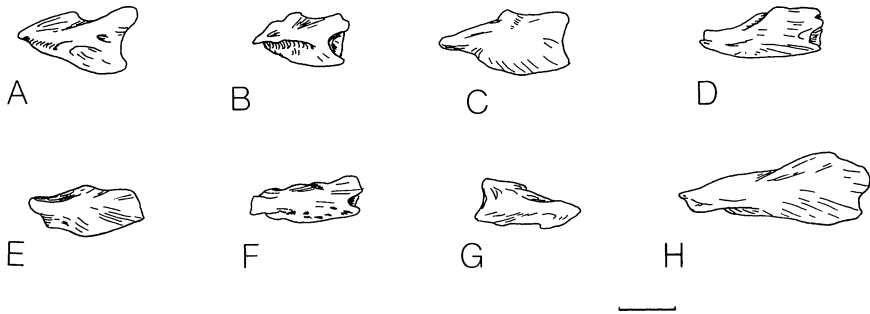
Fig. 28. Interopercles in lateral view. A. *Ictalurus (Ictalurus) punctatus*, UMMZ 186274-S-1. B. *Ictalurus (Ictalurus) lupus*, UMMZ 186503-S-1. C. *Ictalurus (Ictalurus) furcatus*, UMMZ 169031-S-2. D. *Ictalurus (Amiurus) natalis*, UMMZ 186272-S-1. E. *Ictalurus (Amiurus) catus*, UMMZ 186240-S-2. F. *Ictalurus (Amiurus) platycephalus*, UMMZ 186245-S-2. G. *Noturus (Noturus) flavus*, UMMZ 126365-S-1. H. *Pylodictis olivaris*, UMMZ 169029-S-1. Scale 5mm.
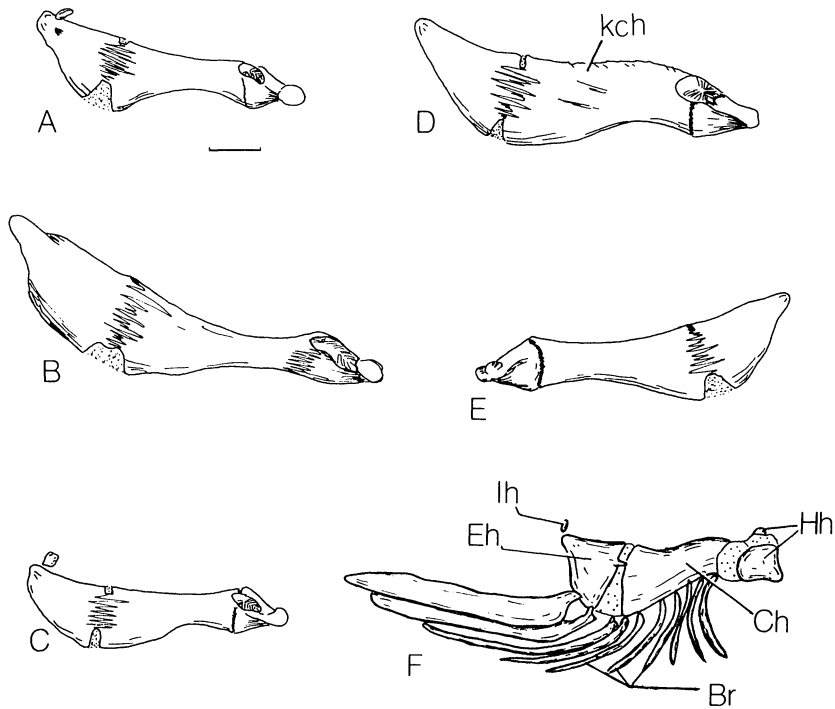
Fig. 29. Hyoid bars. A. *Ictalurus (Ictalurus) furcatus*, UMMZ 169031-S-2. B. *Pylodictis olivaris*, UMMZ 169029-S-1. C. *Ictalurus (Ictalurus) lupus*, UMMZ 186503-S-1. D. *Ictalurus (Amiurus) natalis*, UMMZ 182060-S-4. E. *Noturus (Noturus) flavus*, UMMZ 169029-S-1. F. *Trogloglanis pattersoni*, SIOH51-379-18A. Scale for A–E 5mm, for F 2mm. For abbreviations see text (Materials and Methods).

triangular (Figure 30I). A narrower urohyal (Figures 30A–H) is found in most other catfishes including ictalurids and is probably more primitive.

The pattern of gill arch ossifications in *Trogloglanis* (Figure 31) is common in ictalurids and many other catfishes. This includes: basibranchials, hypobranchials, ceratobranchials, epibranchials, infrapharyngobranchials, and upper pharyngeal tooth plates. The second and third basibranchials are ossified. The first and second arch hypobranchials are present. All five pairs of ceratobranchials are ossified, and of these the first and second each bear a single row of gill rakers anteriorly, numbering 17 and 12 respectively. The third and fourth ceratobranchials each have two rows, one anterior, the other posterior with 11 to 15 rakers. The fifth ceratobranchial has 12 rakers in an anterior row. All gill rakers are short, stout and weakly connected to the bones with connective tissue. The fifth cerato-branchials are expanded basally to form lower pharyngeal tooth plates. Minute teeth are scattered on these plates.

The epibranchials of the first four gill arches are ossified (Figures
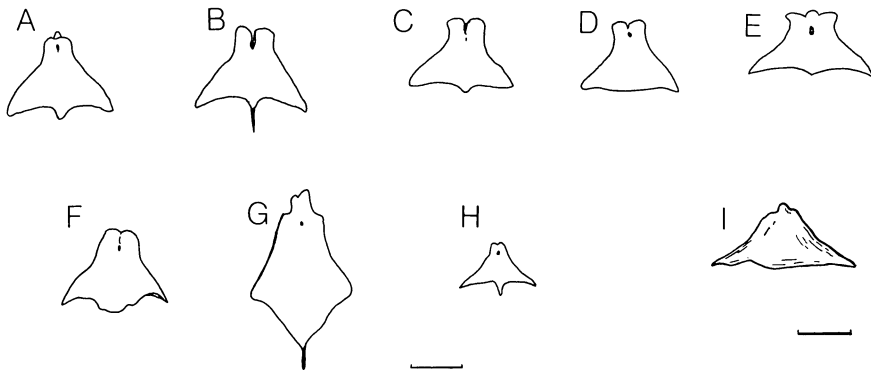
Fig. 30. Urohyals in ventral view. A. *Ictalurus (Ictalurus) punctatus*, UMMZ 186274-S-1. B. *Ictalurus (Amiurus) nebulosus*, UMMZ 171787-S-1. C. *Ictalurus (Amiurus) catus*, UMMZ 186240-S-2. D. *Ictalurus (Amiurus) natalis*, UMMZ 171788-S-1. E. *Ictalurus (Amiurus) brunneus*, UMMZ 186241-S-1. F. *Noturus (Noturus) flavus*, UMMZ 126365-S-1. G. *Pylodictis olivaris*, UMMZ 169029-S-1. H. *Noturus (Schilbeodes) insignis*, UMMZ 165841-S-1. I. *Trogloglanis pattersoni*, SIOH51-379-18A. Scale for A–H 5mm; scale for I 2mm.
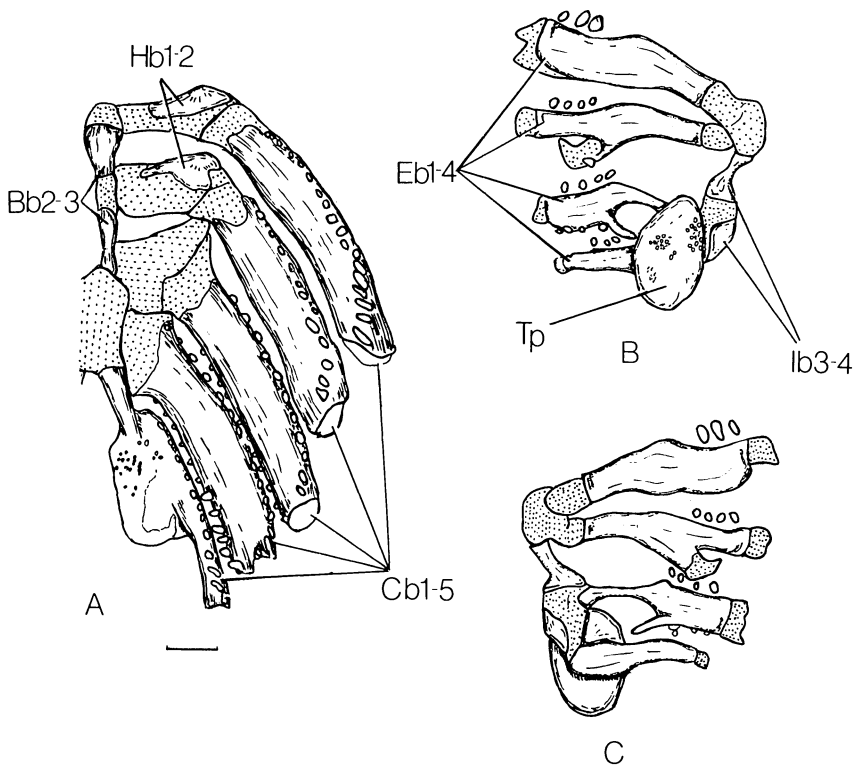
Fig. 31. Gill arches of *Trogloglanis pattersoni*. A. Lower elements in dorsal view. B. Upper elements in ventral view. C. Upper elements in dorsal view. Scale 1mm. For abbreviations see text (Materials and Methods).

31B,C). The first is rod-like and bears a single anterior row of three gill rakers. The second bears a posteromedially directed process and has a row of four gill rakers anteriorly and one raker posteriorly. The third epibranchial bears anterior and posterior rows of rakers, each with four elements, and a slender dorsolateral process. The last epibranchial carries three rakers on its anterior edge. The infrapharyngobranchials of the third and fourth arches are ossified. Below the last two pairs of epibranchials are a pair of large, ovoid upper pharyngeal tooth plates, each with a few tiny scattered teeth.

Total counts of gill rakers on the first arch, all rudiments included, are: *Ictalurus*, 11 or more; *Noturus*, 3 to 10; *Pylodictis*, 10 or more; *Prietella*, 10 to 14; *Satan*, 17 to 19; *Trogloglanis*, 18 to 20 (Taylor, 1969; Suttkus, 1961; and this study). The counts for the troglobites are high for catfishes in general, and *Noturus* have low counts. These extreme counts are likely derived.

VERTEBRAE.—Vertebral counts for *Trogloglanis* and other ictalurids are presented in Table 5. The precaudal and total counts include the first vertebra and the Weberian complex vertebrae (fused second through fourth vertebrae). In three individuals of *Trogloglanis* it has been possible to get accurate counts on precaudal and caudal vertebrae. Catfish species with similar total numbers can be markedly different in counts of the subunits of the column (cf. *Ictalurus furcatus* and *Pylodictis olivaris*).

Trogloglanis has relatively low vertebral counts among ictalurids. These counts are probably derived and likely associated with small body size (Lindsay, 1975). The species closest to *Trogloglanis* in vertebral counts are the smaller members of their respective lineages.

Precaudal vertebrae beginning with the fifth (first in back of the complex Weberian centrum) through the tenth have the transverse processes attached dorsally on their centra (Figures 7, 32B). Caudally on successive vertebrae these processes approach one another and eventually fuse to form hemal arches and spines. The transverse processes are shorter than their associated centra except for those on the fifth vertebra. The transverse processes of the sixth through tenth vertebrae bear short, slender ribs.

The Weberian apparatus of *Trogloglanis* is unique (Figures 7, 32B, cf. 33) probably due to the extreme reduction or absence of the swim bladder. No trace of the swimbladder can be found in any of the *Trogloglanis* examined and this is apparently the case in *Satan* too (Hubbs and Bailey, 1947). It seems that the Weberian apparatus is vestigial, except as it relates to support of the unusually robust dorsal fin pterygiophores and spine. Unlike most catfishes (all but *Diplomystes*, *Prietella*, and *Satan* of those examined) only the first four vertebrae are modified to form the apparatus. The fifth centrum is not sutured to the complex centrum which is composed of the second through fourth centra, fused together as in other catfishes. The first

TABLE 5

MODES AND RANGES OF PRECAUDAL AND CAUDAL VERTEBRAL COUNTS IN
13 SPECIES OF ICTALURIDS SELECTED TO SHOW VARIABILITY OF GENERA.
WITHIN THE SUBGENERA *ICTALURUS* AND *AMIURUS* THE THREE REPRESENTATIVES
SHOW THE MINIMUM, A CENTROID, AND MAXIMUM PRECAUDAL COUNT. THE PRECAUDAL
COUNTS INCLUDE THE FIVE VERTEBRAE INVOLVED IN THE WEBERIAN COMPLEX.
DATA ARE SUMMARIZED FROM LUNDBERG (1970).

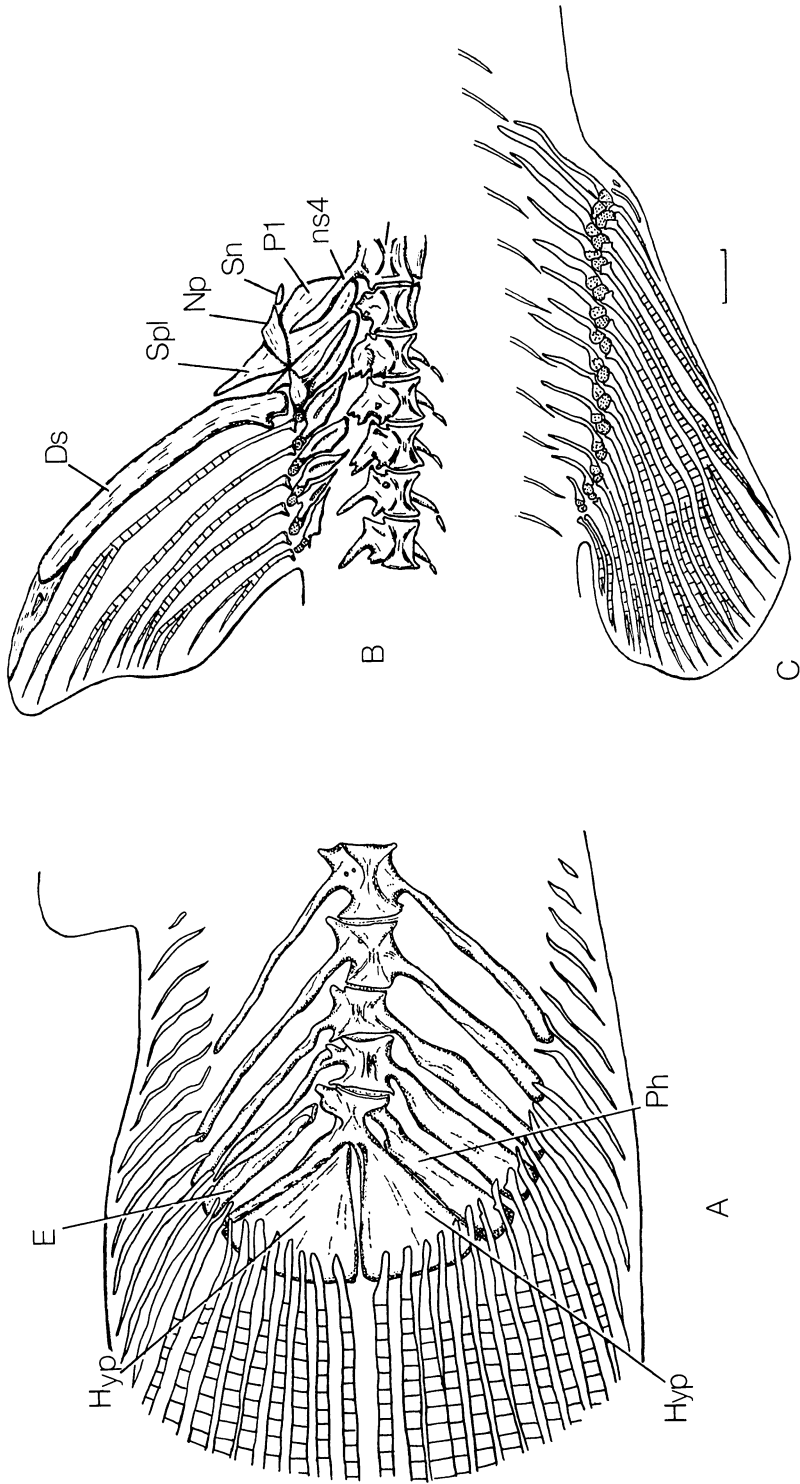|	Precaudal (15 16 17 18 19 20 21 22 23 24)	Caudal (20 21 22 23 24 25 26 27 28 29 30 31 32 33 34)	Sample Size
Trogloglanis pattersoni	X----- (15)	-----X (20–21)	3
Ictalurus			
(*Ictalurus*) *mexicanus*	X---- (17)	-----X---- (26)	13
(*Ictalurus*) *puncatus*	X----------------- (18)	---------------X---- (31)	20
(*Ictalurus*) *furcatus*	-----X---- (19–20)	----X-------- (32)	20
(*Amiurus*) *melas*	-----X---- (16)	--------X-------- (24)	20
(*Amiurus*) *serracanthus*	X---- (17)	-----X---- (25)	19
(*Amiurus*) *catus*	-----X---- (17–18)	--------X-------- (24)	20
Noturus			
(*Noturus*) *flavus*	-----X (18)	--X-------- (24)	16
(*Schilbeodes*) *insignis*	---------X (18)	----X---- (25)	14
(*Rabida*) *stigmosus*	-----X--- (16–17)	-----X-------- (22–24)	14
Prietella phraeatophila	X----- (15)	X---- (22)	3
Pylodictis olivaris	----X---- (22)	-----X-------- (24)	11
Satan eurystomus	X (19)	X (24)	1

Fig. 32. Median fin skeletons of *Trogloglanis pattersoni*. A. Caudal skeleton B. Dorsal fin and associated vertebrae. C. Anal fin. Scale 2mm. For abbreviations see text (Materials and Methods).

centrum is foreshortened, with normal joints on the basioccipital and complex centrum. This centrum lacks neural arches and spine and ventrally it is concave, with a longitudinal trough for the dorsal aorta.

The complex centrum is relatively short compared to other ictalurids. Low ridges at the ventrolateral corners continue the aortic groove caudad. The superficial ossification characteristic of ictalurids (Figures 7, 33B, C) and nearly all other catfishes is lacking. Strong processes project to the supracleithra (not illustrated), like the transverse processes of the fourth vertebra in other catfishes. No bony sheets or shelves lie posterior to these enlarged transverse processes as in other ictalurids (Figure 33A) and the majority of other catfishes. A robust, transversely flattened and bifid neural spine arises dorsally from the complex centrum (Figures 7, 32B, 33C) to form the major supporting strut for the anterior pterygiophores of the dorsal fin. A vertical lamina of bone on the midline is found in front of this neural spine like that of larger species of the family. *Trogloglanis* lacks a separate bone (neural complex, see Weitzman, 1962) above the anterior part of the Weberian apparatus like most ictalurids.

Three pairs of Weberian ossicles are evident (Figure 7). The tripus is a thin splint, loosely attached to the lateral surface of the complex centrum below the transverse process. Probably because the swimbladder is undeveloped, the tripus is not expanded to form a transformator process. Anteriorly the tripus runs upward to terminate lateral to the claustrum, a relatively deep plate above the anterior edge of the first centrum. The scaphium is a minute, ovoid plate, lying in connective tissue posterior to the claustrum, free from the other ossicles. The intercalare, a bony nodule in a ligament between the tripus and scaphium in other catfishes, is lacking.

The function of the chain of Weberian ossicles in catfishes and other ostariophysans is to transmit movements of the swimbladder wall to the inner ear (Alexander, 1964). In *Trogloglanis*, if vibrations of any sort passed along the ossicles, only the tripus and claustrum could be involved. Without a swimbladder, however, the whole functional complex of anterior vertebrae and inner ear, which is so characteristic of the Ostariophysi, seems to have been abandoned. If *Satan* also lacks a swimbladder, paralleled regressive changes in the Weberian apparatus may be found.

The caudal skeleton of *Trogloglanis* (Figure 32A) is highly consolidated (Lundberg and Baskin, 1969). As in other catfishes the first preural and first ural centra are fused to form a compound centrum. Anteriorly the compound centrum bears a well developed neural arch. A single epural lies free above the neural arch. The parhypural is fused to the compound centrum and free from the lower hypurals. (Based on an unclear radiograph Lundberg and Baskin (1969) erroneously reported that the parhypural is fused with the
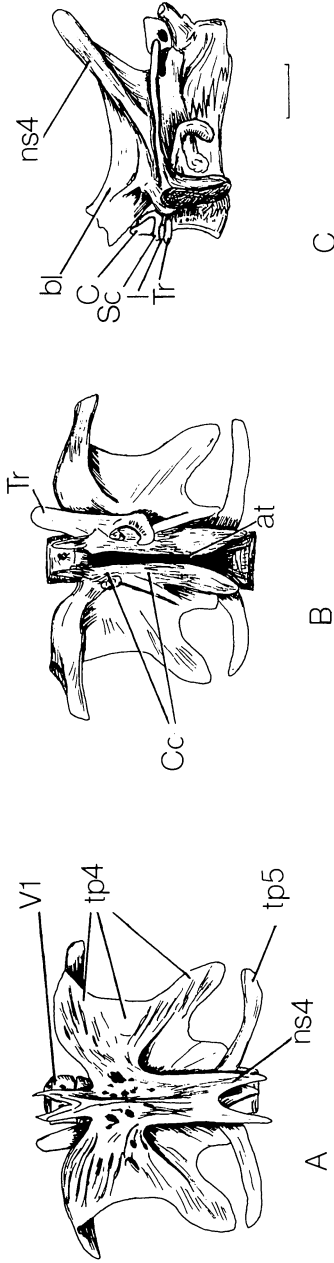
Fig. 33. Weberian complex of *Ictalurus (Amiurus) catus*, UMMZ 186240-S-2. A. Dorsal view. B. Ventral view. C. Lateral view. Scale 5mm. For abbreviations see text (Materials and Methods).

lower hypurals.) The two lower hypurals are fused to one another and to the compound centrum. There is no distinct hypurapophysis on the hemal arch of the parhypural. However, a secondary hypurapophysis is formed on the base of the lower hypurals. The upper hypurals form a fused unit in contact with, but not ankylosed to, the compound centrum and overlying uroneural. There is no trace of second ural centrum material at the base of the upper hypurals.

Ictalurids present a variety of hypural fusion patterns. Most primitive in the family and in siluriforms generally, is the six hypurals and parhypural separate (Figure 34A), found in all species of *Ictalurus, Pylodictis,* some species of *Noturus,* and the extinct genera *Astephus* and *Hypsidoris.* Most species of *Noturus* have lost the uppermost or sixth hypural (Figure 34B) and show intraspecifically variable fusion patterns among the remaining bones. *Prietella* consistently has all lower elements fused and all upper hypurals fused (Figure 34C). *Trogloglanis* and *Satan* are similar to *Prietella* except that in these genera the parhypural is free from the lower hypurals. Loss of the hypurapophysis and retention of the secondary hypurapophysis in *Trogloglanis* is a unique character combination. Most ictalurids have both types of hypuraphophyses.

MEDIAN FIN SUPPORTS.—The dorsal fin of *Trogloglanis* (Figure 32) is supported by one spinelet, one long, defensive spine, and six soft fin rays, internally braced by two hypertrophied, and five normal pterygiophores (basals). The two enlarged pterygiophores support the dorsal spines and are a part of the spine locking mechanism (Alexander, 1965). Each consists of a vertical median plate, and lateral struts under an ornamented, horizontal nuchal plate. The first pterygiophore is clasped below by the enlarged bifid neural spine of the Weberian complex. The nuchal plate of this pterygiophore is cresentic and lies anterior to the spinelet. Behind the plate there is a stout nob formed by fusion of the middle radial with the proximal radial. The spinelet rides over this nob when the fin is moved. The distal radial belonging to the first pterygiophore is fused to the base of the defensive spine.

The second pterygiophore is closely applied to the posterior surface of the first. Proximally it is received by a short bifid neural spine of the fifth vertebra. Distally its nuchal plate forms a saddle and a pair of facets for the spine base. A short process arising from the posterior margin of this plate is directed posteriorly toward the base of the first soft fin ray. This process is capped with a cartilaginous middle radial.

The remaining pterygiophores have a common shape and become progressively smaller posteriorly. Each bears a cartilaginous middle radial. All distal radials are cartilaginous nodules located between the bases of the soft fin rays.

The structure of the dorsal fin supports of *Trogloglanis* is
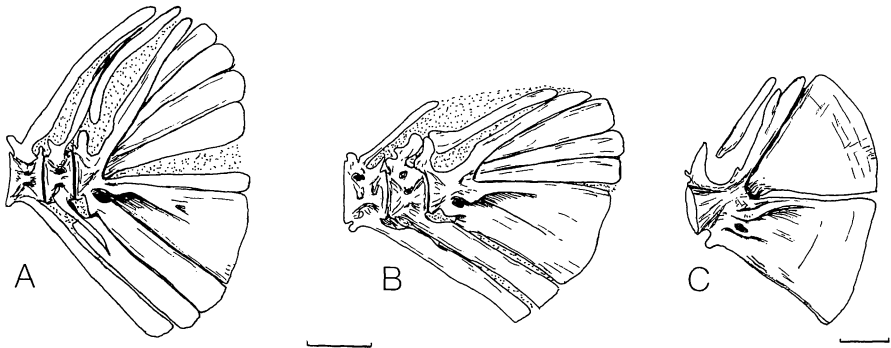
Fig. 34. Caudal skeletons. A. *Ictalurus (Amiurus) serracanthus*, UMMZ 186258-S-1.
B. *Noturus (Noturus) flavus*, UMMZ 182039-S-1. C. *Prietella phreatophila*, UMMZ 173788.
Scale for A, B 3mm, scale for C .25mm.

standard for catfishes with a high and anteriorly placed dorsal fin. It
is probably primitive for ictalurids, and is shared with most species of
Ictalurus (Figures 35A, B), *Astephus*, and *Hypsidoris*. In a few species
of *Ictalurus* and *Pylodictis* (Figure 35C) the first nuchal plate is more
lightly built. And, this structure is much reduced in *Noturus* (Figure
35D) and *Prietella*. The latter genus has lost the V-shaped spinelet
and the dorsal spine itself has almost the character of a soft ray.
Pylodictis, Noturus, and *Satan* share the advanced condition of
concave facets for the dorsal spine on the second pterygiophore.

The anal fin ray counts of *Trogloglanis*, the architecture of this
fin, and its supports are typical for those of catfishes in general
(Figure 32C). Of 17 anal fin rays in the skeletonized specimen of
Trogloglanis, the first three are short and simple, two others are long
and simple and the remaining twelve are branched. There are
fourteen pterygiophores, each consisting of a slender ossified proxi-
mal radial, and cartilaginous middle and distal radials. The first two
fin rays lack support from pterygiophores, and the last pterygiophore
braces two independent fin rays.

PECTORAL GIRDLE.—The pectoral fin rays of *Trogloglanis*
articulate with three radials of which the posterior two are ossified.
The complex joint on the cleithrum (Figure 36) for the spine
conforms to the standard siluriform pattern. The cleithrum is rela-
tively large and meets its antimere on the ventral midline in a long
straight symphysis. The posterior (humeral) process of the cleithrum
is short and devoid of ornamentation on its external surface. The
scapula and coracoid are fused and a mesocoracoid arch is present.
The coracoids of either side join one another on the midline through
about eleven interdigitating sutures. There is a short ventral keel on
the coracoid and its posterior edge is turned sharply upward.

The supracleithrum (Figure 6) has the typical articulations with
the cleithrum below, and posttemporal, epioccipital and pterotic
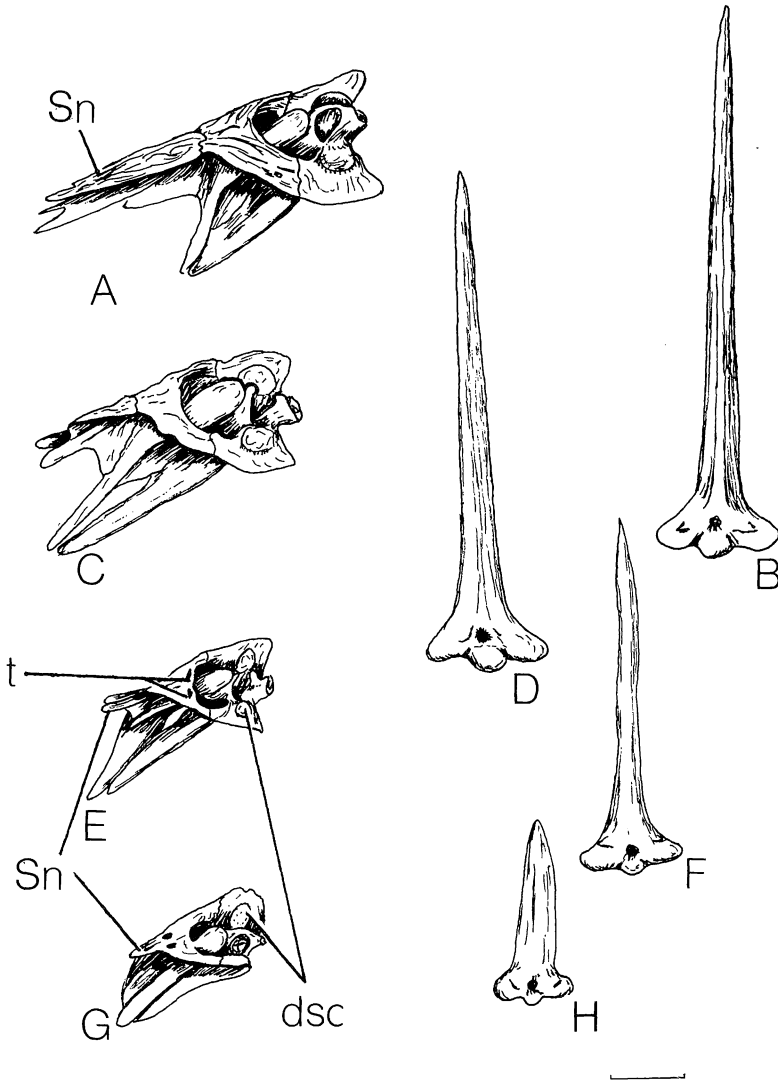
Fig. 35 Anteriormost pterygiophores (basals) of dorsal fins and dorsal spines. A and B. *Ictalurus (Ictalurus) punctatus*, UMMZ 186274-S-1. C. and D. *Ictalurus (Amiurus) catus*, UMMZ 186249-S-2. E. and F. *Pylodictis olivaris*, UMMZ 169029-S-1. G and H. *Noturus (Noturus) flavus*, UMMZ 126365-S-1. Scale 5mm. For abbreviations see text (Materials and Methods).

bones above. The transscapular ligament is nearly completely ossified to its attachment with the basioccipital.

Several features of the pectoral girdle have undergone evolutionary divergence within the Ictaluridae (Figures 36–39). Three basic conditions of the size and ornamentation of the posterior cleithral process are found among catfishes: long and unornamented (Figure
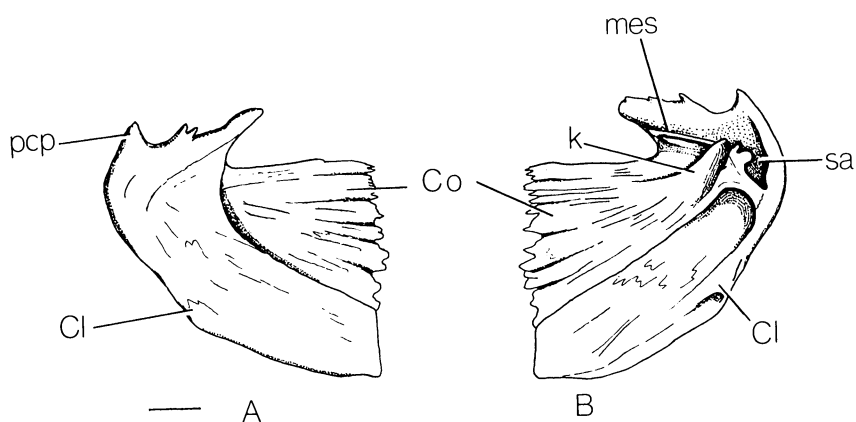
Fig. 36. Right pectoral girdle of *Trogloglanis pattersoni*. A. Dorsal view. B. Ventral view. Scale 2mm. For abbreviations see text (Materials and Methods).
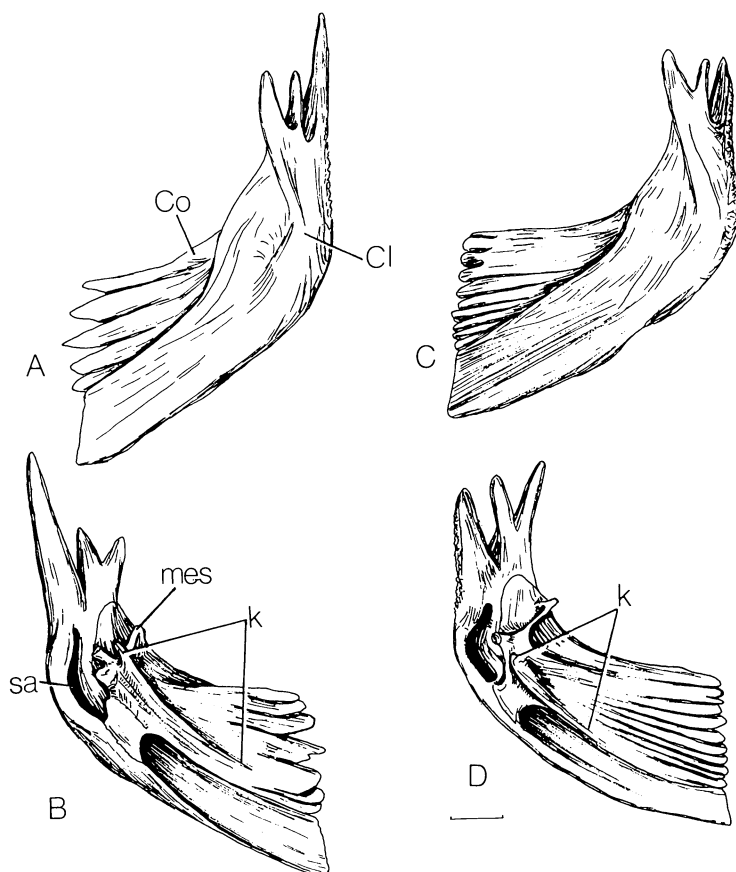
Fig. 37. Left pectoral girdles in dorsal and ventral views. A, B. *Ictalurus (Ictalurus) punctatus*, UMMZ 186274-S-1. C, D. *Ictalurus (Amiurus) catus*, UMMZ 186240-S-2. Scale 5mm. For abbreviations see text (Materials and Methods).
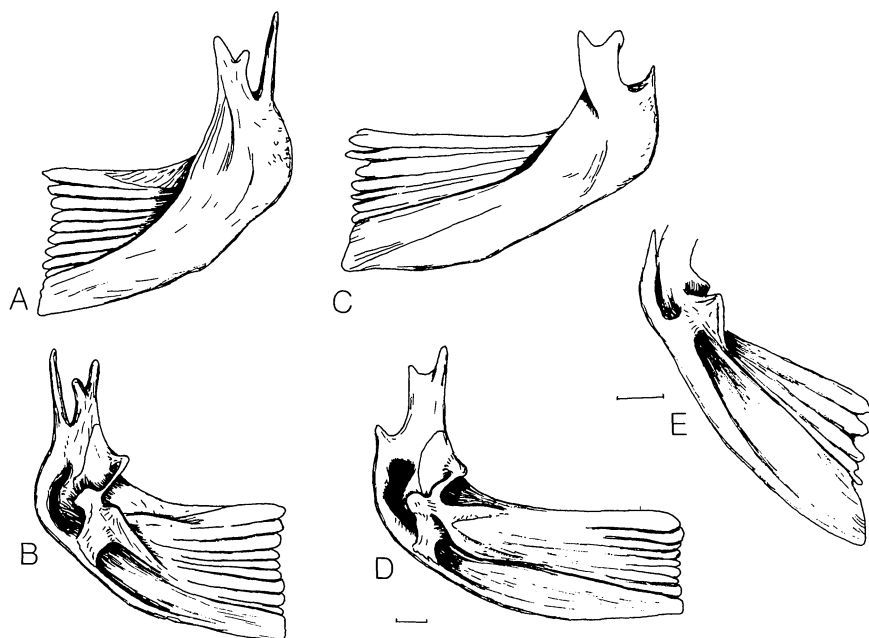
Fig. 38. Left pectoral girdles in dorsal and ventral views. A, B. *Noturus (Rabida) stigmosus*, UMMZ 165841-S-1. C, D. *Noturus (Noturus) flavus*, UMMZ 126365-S-1. Scale for A–D 3mm. E. *Prietella phreatophila*, UMMZ 173788. Scale for E .5mm.

39C), long and ornamented with bony tuberculations (Figures 39D, E, F), and short and unornamented (Figures 39G, H). All three character state combinations are found within a variety of families, suggesting that parallel evolution has occurred. The long and unornamented type of process is likely the most common among siluriforms, and since it is also found in some of the early Tertiary ictalurids (*Astephus*), it is believed to be primitive for the family. *Trogloglanis, Pylodictis, Satan, Prietella* and most species of *Noturus* have short unornamented cleithral processes; most species of *Ictalurus* possess long, ornamented processes. Both character state combinations are thus derived in divergent ways.

The pectoral girdle symphysis, formed by the cleithra and coracoids, is relatively long in *Trogloglanis* compared to most other ictalurids (Figures 36–39). Only some of the bullheads (*Amiurus*) have cleithra as long and with as many coracoid sutures. *Trogloglanis* also is similar to the bullheads, and to *Noturus, Prietella* and *Pylodictis*, in having a short ventral coracoid keel, a relatively primitive condition. This keel is much longer in species in the subgenus *Ictalurus*. In having the posterior edge turned sharply toward the vertical, however, the coracoid of *Trogloglanis* is more like that found in the subgenus *Ictalurus* and some species of *Noturus*
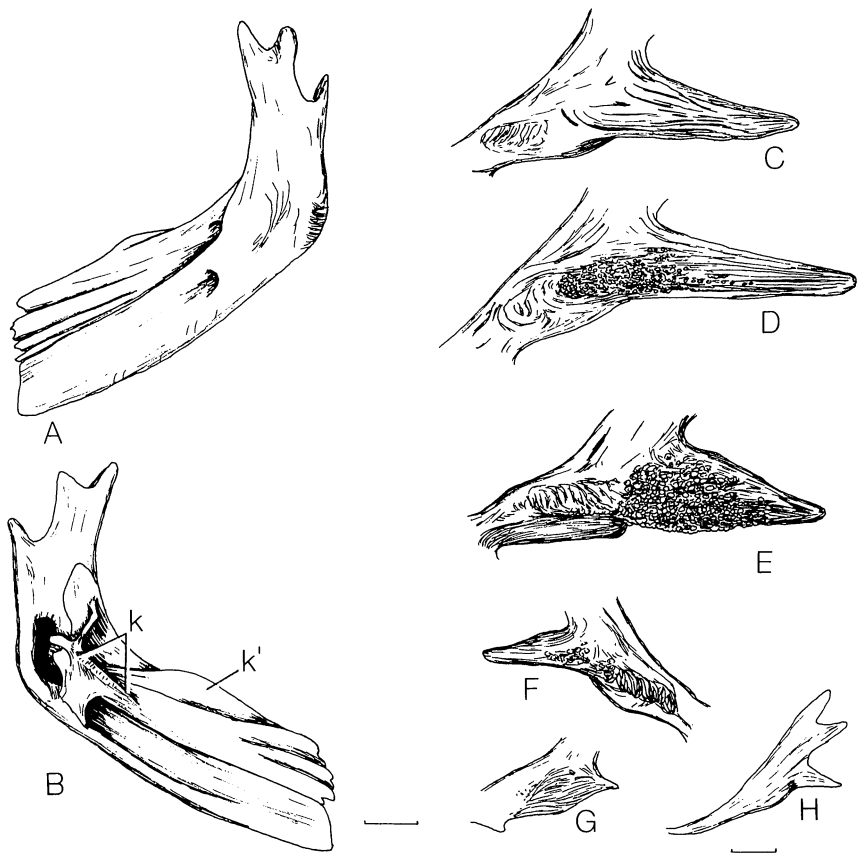
Fig. 39. Left pectoral girdle of *Pylodictis olivaris*, UMMZ 169029-S-1. A. Dorsal view. B. Ventral view. Posterior cleithral ("humeral") processes. C. *Ictalurus (Ictalurus) furcatus*, UMMZ 186263-S-5. D. *Ictalurus (Ictalurus) punctatus*, UMMZ 186271-S-1. E. *Ictalurus (Amiurus) catus*, UMMZ 186252-S-3. F. *Ictalurus (Amiurus) natalis*, UMMZ 182060-S-5. G. *Noturus (Noturus) flavus*, UMMZ 126365-S-1. Scales for A–G 5mm. H. *Prietella phreatophila*, UMMZ 173788. Scale for H 1mm. For abbreviations see text (Materials and Methods).

(e.g., *N. stigmosus*). This is apparently a derived condition because other ictalurids have a much less elevated coracoid margin like that of most catfishes in other families.

The incompletely ossified transcapular ligament is a feature shared by *Trogloglanis*, *Noturus*, *Prietella*, and *Pylodictis*. The presence of this condition in large *Pylodictis* shows that it is not simply a correlate of small body size. Since nearly all other siluriforms have the ligament completely ossified, the former condition is thought to be advanced.

PELVIC GIRDLE.—The pelvic girdle of *Trogloglanis* resembles that in other ictalurids and several other catfish groups
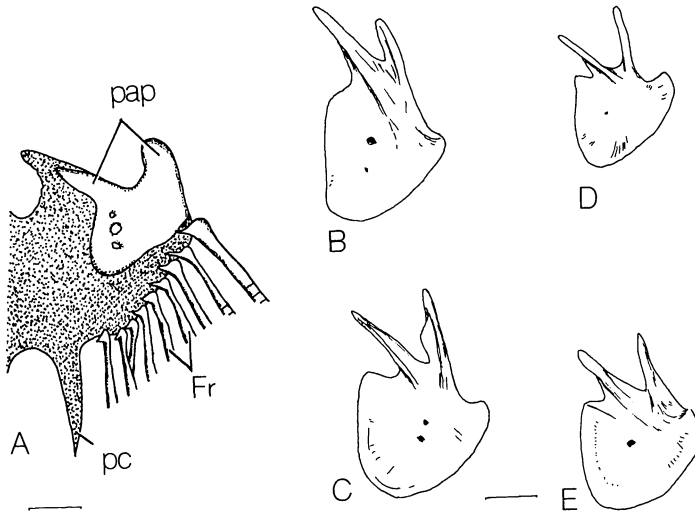
Fig. 40. Left pelvic girdles in ventral view. A. *Trogloglanis pattersoni*, SIOH51-379-18A. Scale 1mm. B. *Ictalurus (Ictalurus) furcatus*, UMMZ 186263-S-5. C. *Ictalurus (Amiurus) nebulosus*, UMMZ 182059-S-5. D. *Noturus (Noturus) flavus*, UMMZ 126365-S-1. E. *Pylodictis olivaris*, UMMZ 169029-S-1. Scale for B–E 5mm. For abbreviations see text (Materials and Methods).

(Figure 40). It is weakly ossified with prominent anteromedial and anterolateral processes. Posteriorly there is an elongate cartilaginous process. Unlike other ictalurids, however, there is no trace of a posterolateral process beyond the outermost fin ray. This appears to be a loss since most catfishes have the process.

INTERNAL SOFT ANATOMY

BRAIN.—The gross structure of the brain of the cleared *Trogloglanis* specimen is visible and can be compared to other fishes (Figure 41). There are no traces of optic lobes or optic tracts (cranial nerve II). Eyed ictalurids have prominent optic lobes and optic tracts. Weisel and McLaurey (1964) discovered normal bilaterally symmetric optic lobes in specimens of *Ictalurus nebulosus* with asymmetrically reduced eyes. The optic tracts in their fish, however, were reduced on the sides which had the defective eye. The condition of the optic lobes and tracts in *Satan* and *Prietella* remains to be worked out. In other blind teleosts, reduction of this part of the brain has occurred, but not to the extreme degree as that in *Trogloglanis*. These include: *Amblyopsis* and *Typhlichthys* (Eigenmann, 1909; Poulson, 1963), *Phreatobius* (Reichel, 1927), *Typhlogarra* (Marshall and Thines, 1958), *Caecobarbus* (Thines, 1969), and *Astyanax* (Stefanelli, 1954; Frank, 1964).
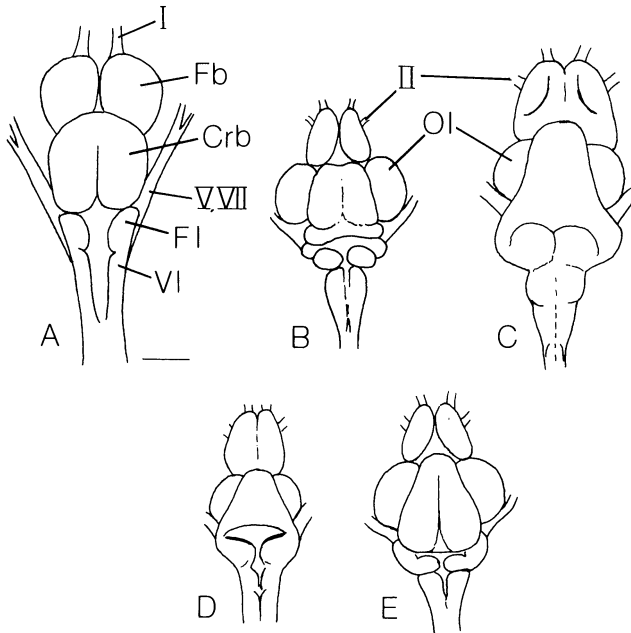
Fig. 41. Brains in dorsal view. Standard lengths of fish in parentheses. A. *Trogloglanis patersoni* (67mm). B. *Ictalurus (Ictalurus) punctatus* (56mm). C. *Ictalurus (Amiurus) natalis* (87mm). D. *Noturus (Schilbeodes) insignis* (67mm). E. *Pylodictis olivaris* (62mm). Scale 2mm. For abbreviations see text (Materials and Methods).

In *Trogloglanis* the facial lobes and vagal lobes appear to be less prominent than in epigean ictalurids. This suggests, contrary to what might be expected, that there has been a trend to reduce the importance of taste in this troglobite. Other ictalurids are known to rely on taste as the receptor for the detection of food at a distance (Todd et al., 1967).

The cerebellum of *Trogloglanis* is prominent but unlike surface-living ictalurids it is rounded in shape. In other ictalurids, and catfishes of other families, the cerebellum has a more trapezoidal form.

Finally, in contrast to the trends toward reduction, *Trogloglanis* has a relatively large forebrain. The forebrain is not proportionately scaled down; each cerebral hemisphere is nearly half the size of the cerebellum. Also, the cerebral hemispheres have a rounded shape. In eyed ictalurids the cerebral hemispheres take the form of an elipse, and they are much smaller relative to the cerebellum. This suggests that the olfactory sense has been maintained in the cave catfish, although the olfactory rosette appears neither hypertrophied nor more complex than in epigean species. In bullheads the olfactory sense is concerned primarily with the detection of pheromones in

highly structured social behavior (Bardach and Todd, 1970). If this is general in ictalurids, retention of a well developed olfactory sense in the troglobite is understandable since population density is probably low, and location of mates might otherwise pose a serious problem. In this regard note that six of the twenty four reported captures of *Trogloglanis* involve two or more individual fishes, suggesting that the troglobites are not solitary.

VISCERA.—*Trogloglanis* lacks a swimbladder. Its stomach and liver are reduced, but the intestine is long and coiled (Figure 42). Large masses of adipose tissue are scattered throughout the mesenteries (and fat deposits are noticeable under the skin). These are the striking differences in visceral anatomy between *Trogloglanis* and other ictalurids. (*Satan* lacks a swimbladder too, but other details of its internal organs remain to be worked out.)

The testes are weakly lobulate in two male specimens as noted by Hubbs and Bailey (1947), a condition similar to that of immature males of *I. natalis*. Mature males of epigean ictalurids have many fine projections born along the lengths of the testes.

The females have paired elongate ovaries, containing several hundred small (0.1 mm) eggs. The uniformly small size of the ova suggests that the females too are sexually immature. The mature eggs
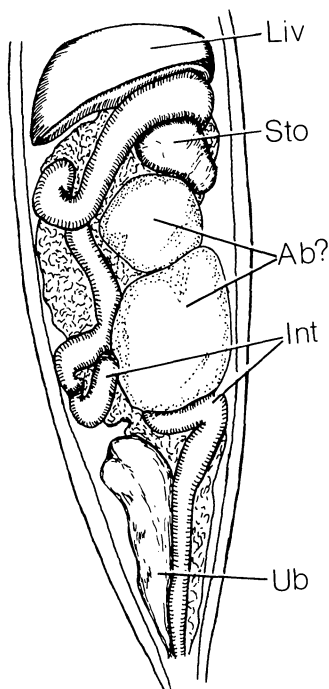
Fig. 42. Viscera in ventral view of *Trogloglanis pattersoni.*

of epigean ictalurids vary among species from about 3 to 6 mm (Jones et al., 1978).

There is a distinct, large urinary bladder in *Trogloglanis* as in other ictalurids.

PHYLOGENETIC ANALYSIS

HISTORY.—In his original description of *Trogloglanis* Eigenmann (1919) stated that this blind fish was most closely related to *Noturus*. Taylor (1969) suggests, and I agree with him, that Eigenmann was probably impressed by the long adnate adipose fin in these forms. *Satan* and *Prietella*, and two other blind ictalurids, with similar adipose fins, were unknown to Eigenmann. He reasonably interpreted the adipose fin form as a unique character state for *Trogloglanis* plus *Noturus*. It now appears, in light of the probable sister group relationship between *Satan* and *Pylodictis*, that the adnate condition of the adipose has evolved independently in *Satan*. Perhaps this character alone is not strong evidence for close relationship between *Noturus* and *Trogloglanis*. In fact, when other characters are considered, there is no compelling evidence to hypothesize a relationship between *Trogloglanis* and *Noturus* without also including certain other groups.

Hubbs and Bailey (1947) also used adipose fin structure, but they argued that *Trogloglanis* was derived from an *Amiurus*-like ancestor. They viewed the adipose as adnate to the back but separated from the procurrent rays of the caudal fin. I find no distinct gap between these fins as there is in *Amiurus*; a well defined bridge of integument connects their margins (Figures 1 and 32A). Hubbs and Bailey also noted that *Amiurus* and *Trogloglanis* lack a venom pore in the axil of the pectoral fin. This condition can be found also in *Ictalurus* and *Pylodictis*, so that it does not appear to relate *Trogloglanis* and *Amiurus* alone.

Suttkus (1961) states that the form of the supraethmoid of *Trogloglanis* resembles most closely *Ictalurus*, especially *I. (Amiurus) melas*. He did not suggest any particular phylogenetic relationship between the two species. The similarity of the supraethmoid between *I. (A.) melas* and *Trogloglanis* involves only the lack of mesial processes on the cornua which are also absent in *Pylodictis* and *Satan*. Beyond this *Trogloglanis* has a uniquely shaped supraethmoid.

Taylor (1969) used several characters to argue for the derivation of *Trogloglanis* from an ancestor "not greatly unlike *I. punctatus*." These are: (1) high, arched skull and short head, (2) long supraoccipital process, (3) many gill rakers, (4) inferior position of mouth, (5) long lateral line canal, and (6) eight pelvic rays.

Not all of the character states on this list are shared only between

Trogloglanis and *I. punctatus*-like (i.e., subgenus *Ictalurus*) catfishes. Eight is a common pelvic fin ray count in *Amiurus*, *Prietella* and some species of *Noturus* (Table 4). Furthermore, being a rather low count among living ictalurids, it is a primitive condition. Similarly the high gill raker count of *Trogloglanis* (18–20) is approached not only in *Ictalurus* (11 or more) but by *Satan* (17–19). And, *Prietella* (10–14) has a high gill raker count compared to its sister group *Noturus* (3–10). These two characters do not argue for a special close relationship (i.e. ancestor-descendant or sister group) between *Trogloglanis* and the subgenus *Ictalurus*.

Concerning the length of the lateral line, I find the short condition of *Trogloglanis* to be most like, and intermediate between, *Amiurus* and *Noturus* (where it ends over or before the caudal skeleton), and the other troglobites (where it ends before the adipose fin origin). In *Ictalurus* and *Pylodictis* the lateral line is complete in terminating at the base of the caudal fin rays.

The remaining three character states on Taylor's list are shared between *Trogloglanis* and the subgenus *Ictalurus*. Two of these, the arched skull and the relatively well developed supraoccipital spine, are likely primitive conditions for catfishes in general and for ictalurids. The prominence of the supraoccipital spine (and the associated supraneural and nuchal plate bones at the dorsal fin origin) in *Trogloglanis* is not without systematic significance. I agree with Taylor that its possession casts doubt on an ancestor in which this apparatus was much reduced. It must be emphasized that it does not, however, indicate a close relationship with *Ictalurus*, because it is primitive for the family.

I feel that *Trogloglanis* has diverged so far in the organization of its mouthparts that a comparison to *Ictalurus* on the basis of mouth position alone might be questioned. The inferior mouth of *Trogloglanis* is caused by the great expansion of the premaxillae and especially by the transverse orientation of the lower jaws. In contrast, the inferior mouth of members of the subgenus *Ictalurus* seems to result more from an elongation of the entire snout (Lundberg, 1970). Nevertheless, the immediate ancestors of *Trogloglanis* must have possessed a relatively short mandible and inferior mouth, perhaps not too unlike channel catfishes. But, this too is likely a primitive condition for ictalurids. Many generalized catfishes outside of the Ictaluridae, especially in the Bagridae, Pimelodidae, and *Diplomystes*, have a subterminal or inferior mouth. And, within the family at least one early lineage, *Hypsidoris*, had such a mouth.

It is noteworthy that systematists have favored relationships between *Trogloglanis* and single genera or subgenera of epigean catfishes: *Noturus*, or *Amiurus*, or *Ictalurus*. *Satan* is obviously the closest relative of *Pylodictis* alone (Hubbs and Bailey, 1947; and see below). *Prietella* is probably the sister-group of the entire genus

Noturus (Taylor, 1969; and see below). However, the possibility can not be dismissed that *Trogloglanis* may be the monotypic sister-lineage of a group of ictalurid genera. This possibility is explored below.

RELATIONSHIPS AMONG ICTALURIDS.—In previous studies I concluded that the likely interrelationships among the major ictalurid groups are as shown in Figure 3 (Lundberg, 1970, 1975a). The evidence for this conclusion is reviewed below, but first a comment on methodology is in order.

To assist in the construction of the phylogeny the "WAGNER TREE" computer program written by J. S. Farris was used. Details of this computer method and applications can be found in Kluge and Farris (1969), Farris (1970), Farris, Kluge and Ekhardt (1970), Lundberg (1972), and Kluge (1975). The algorithm of the computer program is consistent with current phylogenetic reasoning (Hennig, 1966; Wagner, 1969; Farris, Kluge and Ekhardt, 1970). Evolutionary trends of individual characters are specified. Ancestors of every inferred monophyletic group are reconstructed, so that shared derived states are made explicit. Overall, the favored phylogenetic hypothesis is that which requires the minimum amount of evolutionary change, i.e., the lowest total of unique plus parallel plus reversed character state changes. The rationale for this "parsimony" criterion is that it guarantees the correct tree if the block of cladistically correlated characters in the data at hand is larger than any block of *correlated* homoplasious characters. *Uncorrelated* homoplasious characters, even if relatively numerous, introduce inconsequential noise to the task of phylogeny reconstruction.

If particular characters are known to be poor indicators of relationships because of parallel evolution, they should be discarded or given low weight. In general, there are no foolproof a priori criteria by which to recognize homoplasious characters. In this study, however, there are two kinds of characters which almost certainly are not reliable for phylogenetic inference (see also Hecht and Edwards, 1976). First, there are characters that involve derived states which are clear special adaptations to permanent cave life. These features, such as the lack of eyes and pigment, are widely scattered among well founded monophyletic higher taxa but only in troglobites and advanced troglophiles. Second, there are character states that are consequences of a single allometric phenomenon: small size. Such size dependent features would be reliable indicators of relationships only if size itself is, but size is apparently not. Both of these kinds of characters when they can be recognized as such are treated cautiously herein.

The evidence for the hypothesis of interrelationships shown in Figure 3 is reviewed below as a set of annotated lists of shared derived

character states. The character states given are those which probably evolved during the origin of the most recent common ancestor of each monophyletic group. This does not say that every descendant subgroup or species possesses exactly that character state, because frequently subsequent evolution to an even more derived condition occurs. The letter labels of the lists and ancestral intervals in Figure 3 correspond.

(A) Subgenus *Ictalurus*.—Although the Mexican populations pertaining to this subgenus need critical review, a group nominally comprises the living species: *I. furcatus, I. balsanus, I. punctatus, I. lupus, I. dugesi, I. pricei, I. autralis, I. mexicanus,* and *I. meeki.* I have not seen material of *I. meeki.* Following Alvarez (1966) I have regarded *I. ochoterenai* as a synonym of *I. dugesi,* and following examination of material I consider *I. meridionalis* a synonym of *I. furcatus.* In addition, four extinct taxa belong here: *I. rhaeas* from the Oligocene, *I. echinatus* and *I. lambda* from the Pliocene (Lundberg, 1975a) and a Pleistocene species related to *I. dugesi* (Smith, in press). *I. catus* has been included in the subgenus *Amiurus* (see below).

The evidence arguing for a monophyletic status for the subgenus *Ictalurus* is the following set of derived features. These features evolved in the common ancestor of the group and have variously undergone further divergence within it (Lundberg, 1970). Unless stated otherwise these conditions appear to be unique and unreversed.

(1) The superficial parts of the supraoccipital bone are ornamented primarily with longitudinal ridges and grooves (Figures 8–10). Irregular pits are absent. This same condition has evolved in parallel in *Pylodictis* (Figure 18).

(2) The spine on the sphenotic margin is small or absent (Figures 8–10).

(3) There are many sutures between the prootic and basioccipital, and the prootic and exoccipital (Figures 8, 9, 14A).

(4) The optic foramen is large (Figures 8, 9, 14A). This foramen may be secondarily reduced in *I. lupus.*

(5) There is a well developed lateral shelf on the premaxilla (Figures 8–10). More extreme but similar shelves on this bone are found in *Pylodictis* (Figure 18) and *I. (Amiurus) brunneus.*

(6) The premaxillary teeth are distinctly graded in size with the largest teeth anteriorly. *I. (Amiurus) brunneus* among the bullheads has also developed this type of dentition.

(7) The palatine bone is relatively long (Figure 21C). At least some species of *Noturus* have equally elongate palatines.

(8) The outer foramen of the facial canal in the hyomandibular is superimposed on the mandibularis foramen (Figure 25A).

(9) The crest for attachment of levator operculi on the hyomandibular is large (Figure 25A).

(10) The hyomandibular-metapterygoid suture is short (Figure 25A).

(11) The preopercle is expanded and flattened behind its sensory canal (Figure 25A). *Amiurus* and *Noturus* also have an expanded preopercle but in these fishes the expanded part is concave, not flat (Figures 24A, 26A).

(12) The endopterygoids are small (Figures 25A). Equally reduced endopterygoid bones are found in *Noturus* (Figure 26A), and they are lost in some species of *Noturus, Prietella* (Figure 26B), and *Trogloglanis* (Figure 23A).

(13) The modal anal fin ray count is at least 22 (Table IV). Anal fin ray counts have undergone much parallel evolution and three bullheads have modal counts of 22 or more: *I. nebulosus, I. catus* and *I. natalis.*

(14) The ventral keel of the coracoid is long (Figure 37B).

(15) The pectoral spines become flattened with attainment of large body size. This is known with certainty only in *I.* furcatus and *I. punctatus.*

(16) The posterolateral process of the pelvic girdle is small.

(B) *Amiurus, Noturus, Prietella, Pylodictis* and *Satan.*— Together these five major ictalurid lineages form a monophyletic group. The evidence for this consists of the block of derived character states listed below which arose in an inferred ancestor of these five taxa. It follows that the genus *Ictalurus* is a paraphyletic taxon since *Amiurus* has a more recent common ancestry with, and is the sister group of *Noturus + Prietella + Pylodictis + Satan* than the subgenus *Ictalurus.* Most of the similarities between the subgenus *Amiurus* and *Ictalurus* are due to shared primitive character states.

(1) The caudal fin is nearly always emarginate or truncate (Figure 3); never deeply forked with pointed lobes. The only species with a distinctly lobed tail in this group is *Ictalurus (Amiurus) catus,* and interpreted parsimoniously this seems to be an evolutionary reversal, i.e., the most recent common ancestor of *Amiurus* had an emarginate or truncate caudal fin.

(2) The supraoccipital spine is relatively narrow and falls well short of contacting the supraneural (Figures 11–19). In many members of this lineage the supraoccipital spine is further reduced. This feature is apparently developed independently within the subgenus *Ictalurus* in *I. dugesi, I. lupus* and *I. balsanus.*

(3) The upper limb of the preopercle is truncated such that it does not extend above the adductor crest of the hyomandibular (Figures 24, 25G, 26).

(4) The suprapreopercle is always fragmented into two parts. Occasionally it is lost.

(5) The bases of proximal posterior dentations on the pectoral spine arise from the dorsal half of the spine shaft (Figure 4C). Rare

exceptions to this appear where the dentations become very large (e.g., subgenus *Rabida* in *Noturus*).

(6) The skull roof is at least slightly flattened (never highly arched). Some members of this lineage have carried on this trend to extreme skull depression (e.g. *I. (A.) platycephalus* and *brunneus, N. flavus, Satan* and *Pylodictis*).

(7) The wing of the lateral ethmoid is short and nearly horizontal; not curved downward (Figures 14B, 19).

(8) There are 7 infraorbital bones (Figure 20B) as opposed to variably 6 or 7 within species of the subgenus *Ictalurus*. As far as known *Prietella* is exceptional in having only 6 infraorbitals, but this could be related to the interruption of the sensory canal found only in this species.

(9) The nasal bone is a wide tube (Figures 11, 12, 15–18).

(10) The upper limb of the supracleithrum is obliquely truncated for attachment of epaxial muscle (Figures 12, 15–18). A similar condition has developed independently in *I. furcatus* and *I. balsanus* of the subgenus *Ictalurus*.

(11) The mandibles and hyoid bones are relatively long, reflecting an increase in breadth of the gape.

(12) Sutures are present between the quadrate and hyomandibular, and quadrate and metapterygoid (Figures 24, 25C, 26).

(13) The interopercle is not expanded posteroventrally (Figure 28).

(C) Subgenus *Amiurus.*—This well defined group includes the living species *I. catus, I. serracanthus, I. platycephalus, I. brunneus, I. natalis, I. melas* and *I. nebulosus.* In addition to the living forms, *Amiurus* is well represented in the fossil record with eight extinct species (Lundberg, 1975a, Baumgartner, 1982). The group appears to be monophyletic on the basis of the following shared advanced character states.

(1) The muscle crests on the frontal meet the margin of the skull roof anterior to the level of the epiphyseal bar, and there is a dorsolateral trough on the edge of the frontal below the infraorbital sensory canal exit (Figures 11, 12, 14B). This trough reflects a unique anterior extension of the attachment of the levator arcus palatini.

(2) The orbitosphenoid bears prominent horizontal shelves of bone (Figure 13, 14B).

(3) The dentary bears a prominent anteroventral crest of bone (Figure 22E).

(4) The coronoid process has a steeply inclined posterior margin at all stages of development (Figure 22E).

(5) The premaxilla is broad and usually bears a small process at the midline. *Pylodictis* has evolved an equally broad premaxilla.

(6) The deepest layer (A_3) of the adductor mandibulae is always split to form an adductor tentaculi. This condition is found in some

species of the subgenus *Ictalurus* also. This is a special muscle which retracts the unique maxillary barbel of catfishes. It is, therefore, obviously a derived feature relative to non-siluriforms. The muscle has a spotty distribution among catfish families which suggests considerable homoplasy in its evolution.

(7) The ceratohyal bears a prominent dorsal keel of bone (Figure 29D).

(D) *Noturus, Prietella, Pylodictis, Satan.*—The monophyletic status of this group of genera is supported by the following derived features. These are shared as stated, or there may be more derived conditions in some member taxa. The osteology of *Satan* is incompletely known at present so that this list may eventually need revision.

(1) The transverse crests along the rear margin of the skull are emarginated at the base of the supraoccipital spine (Figures 15–18). This reflects a broad expansion of the epaxial muscles near the midline.

(2) The supraoccipital spine is very narrow (Figures 15–18).

(3) The supraneural is fused to the first dorsal pterygiophore (Figures 35E, G).

(4) The sphenotic bone does not extend anteriorly beyond the level of the epiphyseal bar (Figures 15–18).

(5) The margins of the parasphenoid stem are not markedly tapered below the orbits (Figures 15, 16, 18).

(6) The anterior part of the ascending parasphenoid wings are vertically oriented below their suture with the pterosphenoid (Figure 19).

(7) There are no bony shelves on the orbitosphenoid (Figures 15, 16, 18, 19). These shelves have been lost independently in some species of the subgenus *Ictalurus* (Figure 14A).

(8) The number of pores of the mandibular sensory canal is usually seven or eight. There are a few exceptional species of *Noturus* and *Prietella* which have the primitive count of six mandibular pores. If these low counts are not secondary reductions, the higher counts have developed independently.

(9) The anterior most pores of the mandibular canal are closely approximated at the mandibular symphysis. *I. (Amiurus) natalis* has evolved this feature in parallel.

(10) The dorsal edge of the adductor crest on the hyomandibular is below the level of the opercular facet (Figures 25C, 26).

(11) The Weberian complex is relatively shallow. This is reflected also in having the transverse process of the fourth vertebra little expanded distally. Both features represent a more depressed form of the predorsal area of the body than is found in other ictalurids. The flat bullheads, *I. brunneus* and *I. platycephalus*, parallel the *Noturus-Pylodictis* group in these derived conditions.

(12) The first dorsal fin pterygiophore is lightly constructed and the second has markedly concave facets for reception of the dorsal spine (Figures 35E, G). *Prietella* is exceptional here in that the dorsal spine facets on the second pterygiophore are not hypertrophied in keeping with reduction of the spine.

(13) The posterior process of the cleithrum is very short (Figures 39G, H).

(14) The transcapular ligament of the supracleithrum is incompletely ossified (Figures 15–18).

(E) *Noturus* and *Prietella*.—Taylor (1969) suggested that these two genera are closely related, and his conclusion is supported by evidence gathered in my studies. *Noturus* and *Prietella* share the following advanced character states which presumably developed in their common ancestor.

(1) The adipose fin is adnate to the back and at least partially joined to the caudal fin. Similar conditions have appeared independently in *Satan* and *Trogloglanis*.

(2) The supraoccipital spine is obsolescent (Figures 15–17).

(3) The longitudinal supraoccipital crests are low, rounded and devoid of ornamentation (Figures 15–17). In *Amiurus* some species have similarly reduced crests, and the troglobites *Satan* and *Trogloglanis* have obsolescent crests.

(4) The laminar component of the posttemporal bone is absent (Figures 15–17).

(5) The wing of the pterotic bone is rounded rather than angular (Figures 15–17).

(6) The margin of the adductor arcus palatini scar on the parasphenoid is continuous with the ventral margin of the bone (Figures 16, 19A).

(7) The endopterygoid is greatly reduced in size (Figure 26). The subgenus *Ictalurus* parallels the *Noturus-Prietella* group in this feature.

(8) The pectoral radials are usually partially fused within species. *Noturus flavus* is an exception but perhaps this is secondary.

(9) The subpterotic process of the supracleithrum is weakly developed (Figures 15–17).

(10) The pelvic splint is vestigial or absent. This is also the case in *Trogloglanis*.

(F) *Noturus*.—This genus comprises 26 species (Taylor, 1969; Jenkins, 1976). The fossil record of *Noturus* is poor consisting only of two Pleistocene finds (Ossian, 1973; Eshelman, 1975; Lundberg, 1975a). Not all species have been studied osteologically but enough is known to support Taylor's division of the group into three subgenera: *Noturus, Schilbeodes* and *Rabida*. Also, the following advanced character states can be offered as tentative evidence for the monophyletic status of the genus.

(1) The eye is subcutaneous.

(2) The foramen for the superficial ophthalmic nerves between the frontal and lateral ethmoid are large (Figures 15–17). *I. furcatus* of the subgenus *Ictalurus* has developed this condition independently (Figure 8).

(3) The orbital foramen in the lateral ethmoid wing is placed anteriorly, just behind the palatine facet (Figure 19A).

(4) The sublateral process of the premaxilla is enlarged and generally toothed (Figures 15, 17, 19A). No lamina of bone connects this process to the posterolateral corner of the premaxilla as in *Pylodictis*.

(5) The opercle is extremely narrow, and the angle between the dorsal and anterior edges is oblique, ca. 128° (Figure 27E).

(7) The number of hypurals is usually reduced through loss of the uppermost bone and through intraspecifically variable fusion among the remaining elements (Figure 34B).

(8) The hypurapophyses are small (Figure 34B).

(9) There is a variable increase in the number of caudal rays.

(G) *Prietella.*—The Mexican blindcat, *Prietella phreatophila*, presents a long list of advanced features relative to its sister group *Noturus.* First, it has adaptations to cave life shared with *Satan* and *Trogloglanis* (see page 00 below). These shared features have arisen by parallel evolution.

(1) Eyes are absent.

(2) The skin lacks pigment.

(3) The body lateral line canal is short, and there are few or no ring-like ossicles associated with it.

(4) The gill raker count (10–14) is relatively high.

Second, perhaps resulting from small size and concomitant paedomorphosis of the skeleton, *Prietella* has the following additional derived features.

(5) Muscle crests on the hyomandibular are weak or absent (Figures 26C, D). This includes the levator arcus palatini crest, levator operculi crest, and adductor hyomandibularis process.

(7) Sutural joints between bones of the suspensorium are reduced (Figures 26C, D).

(8) The sublateral process of the premaxilla is wanting (Figure 17B).

(9) The endopterygoid bone is absent (Figure 26C, D).

(10) The superficial ossification associated with the Weberian apparatus is reduced and the fifth centrum is not sutured to the complex centrum.

Finally, *Prietella* has the following uniquely derived character states which do not necessarily associate with cave life or paedomorphosis.

(11) The anterior cranial fontanelle is nearly closed by weak

sutures between the frontals, and the frontal part of the posterior cranial fontanelle is similarly reduced (Figure 17B).

(12) The preopercular sensory canal is interrupted between the pterotic and preopercle. This results in a pore count of 11, and loss of the suprapreopercle.

(13) The infraorbital sensory canal is interrupted lateral to the frontal so that the pore count is 8 instead of the usual 7 (Taylor, 1969).

(14) The dorsal fin spinelet is absent and the dorsal spine is reduced such that it approaches the structure of a soft fin ray. Correlated with this the first two dorsal pterygiophores are hardly hypertrophied.

(15) The upper and lower hypurals are coossified into two separate plates (Figure 34C).

(16) Principal caudal fin rays are reduced to 7 upper and 8 lower.

(17) The pectoral spine (Figure 5J) base is typically formed, but the shaft halves are not completely fused and distally they are segmented much like a soft ray. Ornamentation of the spine is lacking.

(H) *Pylodictis* and *Satan.*—A close relationship between these monotypic genera has been suggested by Hubbs and Bailey (1947), Suttkus (1961) and Taylor (1955, 1969). Despite the superficial cavernicolous adaptations of *Satan*, its overall similarity to *Pylodictis* is obvious. Furthermore, at least a few shared derived character states can be presented as evidence for their interrelationship. Presumably more similarities will be discovered when *Satan* is more thoroughly studied.

(1) The gill membranes are distinctly overlapped.

(2) The supraethmoid bone has a unique form: broad with widely divergent cornua (Figures 18, 19B).

(3) The skull is depressed and its roof is flat (Figures 18, 19B).

(4) The nasal bone is exceptionally broad and flattened (Figure 18A). A similar type of nasal bone has evolved independently in some bullheads (Figure 12).

(5) The number of mandibular sensory canal pores is 7 or 8.

(6) The first mandibular canal pores have a common opening in a median pit or they are united.

(7) The coronoid process is very low (Figure 22F).

(8) There is an enlarged posterior process on the angular bone (Figure 22F).

(9) The number of pectoral rays is increased to a mode of ten or eleven.

(10) The number of pelvic rays is increased to nine or ten.

(I) *Satan.*—Like the other troglobites in the Ictaluridae, *Satan* has many advanced conditions not also found in its sister group. The same cavernicolous adaptations listed for *Prietella* above are present in *Satan*. In addition, head musculature is somewhat reduced and it

can be predicted that corresponding muscle crests will be weakly developed. Along these same lines of reduction, it is known through radiographs that superficial ossification of the Weberian complex is not well developed, and the fifth centrum is not fused to the complex centrum. Like *Trogloglanis*, the swimbladder is lost, or it may be thin-walled and filled with adipose tissue. Like *Prietella*, the hypurals are consolidated into just two separate plates, the lower plate including the parhypural.

(J) *Pylodictis*.—In overall anatomy *Pylodictis olivaris* is the most divergent epigean ictalurid. In spite of its advanced nature, fossils of the flathead catfish from middle Miocene rocks are taxonomically inseparable from the modern species, indicating early divergence from *Satan* and other ictalurids followed by evolutionary stasis. The list presented here includes the character states of *Pylodictis* that are clearly derived relative to other members of the family.

(1) The posterior cranial fontanelle is nearly completely closed (Figure 18A).

(2) The transverse crests on the rear margin of the skull are tilted obliquely forward at the base of the supraoccipital process (Figure 18A). This indicates more extensive epaxial muscle invasion of the skull than in other ictalurids.

(3) The sphenotic process is large and angular (Figure 18).

(4) The lateral ethmoid wing bears a bony anterior flange above the palatine condyle (Figures 18, 19B).

(5) The parasphenoid stem is much broader than the orbito-sphenoid (Figures 18B, 19B).

(6) The optic foramen is divided by an osseous bridge between the pterosphenoid and parasphenoid (Figure 19B).

(7) The symphyseal process on the dentary is enlarged, and the band of teeth at the symphysis is very broad (Figure 22F).

(8) The sublateral process of the premaxilla is long and toothed. A thick shelf of bone joins this process to the posterolateral corner of the bone (Figure 18).

(9) The jaw teeth are uniformly small and sharply recurved (Figure 18).

(10) The levator arcus palatini crest is prominent. It extends beyond the hyomandibular onto the metapterygoid (Figure 25C).

(11) The levator operculi crest is absent (compare Figures 24A and 25C).

(12) The lower end of the facial canal is superimposed on the mandibularis foramen, plus a bony bridge between the preopercle and hyomandibular divides their common external operning (Figure 25A).

(13) The quadrate-metapterygoid suture is elongate (Figures 25C, D).

(14) The metapterygoid shape is pentagonal with nearly straight ventral and dorsal edges (Figures 25C, D).

(15) The contact between anterior and posterior ceratohyals is primarily sutural (Figure 29E).

(16) The ceratohyal is round in cross section. The ventral edge of the epihyal is expanded and its interopercular facet is large (Figure 29E).

(17) There are many sutures between the ceratohyal and ventral hypohyal.

(18) The urohyal has a rhomboidal form (Figure 30G).

(19) The interopercle is long and slender (Figure 28H) with a deep medial concavity for reception of the epihyal and interhyal.

(20) There is a prominent vertical lamina on the complex Weberian vertebra.

(21) The number of precaudal vertebrae is greatly increased (modally 23 or 24).

(22) Pectoral ray count is modally 11. This is higher than in all other ictalurids except *I. balsanus* which also has 11 pectoral rays.

(23) The pectoral spine has an unossified fiberous tip (Figure 5E).

(24) The anterior serrae of the pectoral spine are large and irregular. The posterior dentations of the spine are large, irregular and often multicuspid (Figure 5E).

A NEW IDEA ON THE RELATIONSHIPS OF TROG- LOGLANIS.—The problem of placing *Trogloglanis* into the ictalurid genealogy is reducible to the usual task of comparing patterns of shared derived character states (synapomorphies of Hennig, 1966). In this regard, however, *Trogloglanis* presents special difficulties. Some of its character states are obvious adaptations to permanent cave life (Section I below) and can be found in troglobites generally. Another large block of features of *Trogloglanis* relate almost surely to its diminutive size and are paedomorphic (Section II below). Such features have questionable value in ascertaining relationships because they are expressions of but a single trend (e.g. Hecht and Edwards, 1976). *Trogloglanis* also presents a long list of specializations that are uniquely derived within the Ictaluridae (Section III below). Such character states (the autapomorphic states of Hennig, 1966) are useless in the search for a sister group.

Subtracting the above three blocks of character states, plus some relatively primitive conditions (Section IV below) which have mini- mal (but not zero) phyletic significance, *Trogloglanis* offers little unequivocal evidence on its systematic position. This evidence shall be discussed after a brief review of the character state blocks I–IV just noted.

I. General troglobitic adaptations shared in the Ictaluridae by *Trogloglanis, Prietella* and *Satan* are as follows.

(1) Lack of eyes.

(2) Lack of pigment.

(3) Short body lateral line canal (Figure 1).

(4) Relatively high number of gill rakers (Figure 31). This last condition is the only one of the four that is not "regressive". The increase in gill raker number may be related to a shift towards a diet including smaller detrital particles than is usual for epigean ictalurids.

II. The features of *Trogloglanis* which are correlates of small size are listed next. Many of these are shared with the other ictalurid troglobites and as such reflect adaptation in size to cave life. However, some of these character states are approached by small species of *Noturus* too. Also, since similar conditions can be found in the young of even the largest ictalurids, they can be regarded as paedomorphic.

(1) Reduced head and body musculature. It is noteworthy, however, that in *Trogloglanis*, muscles of the pectoral and dorsal spines are not reduced.

(2) Weakly ossified skull roof (Figure 6). This includes thin, unornamented dermal bones, lack of the dermal part of the lateral ethmoid, and lack of the lateral bony shelves on the frontals, sphenotic and pterotic.

(3) Lack of sutures between neurocranial bones, especially those of the otic and occipital series (Figure 7).

(4) Incomplete ossification of the parasphenoid wings (Figure 7).

(5) Lack of sutures between bones of the suspensorium (quadrate, hyomandibular, metapterygoid) (Figure 23). It has been noted that catfishes primitively lack sutures between these elements, but I do not believe that paedomorphosis should be ruled out as an explanation for their absence in *Trogloglanis*.

(6) Truncation of upper part of the preopercle and lack of expansion of the preopercle for muscle attachment posterior to its sensory canal (Figure 23). Lack of the suprapreopercle can be noted here too. All of these features could be a part of the weakly ossified condition of *Trogloglanis*. It should be recalled, however, that truncation of the preopercle upper limb and reduction of the suprapreopercle by fragmentation are derived conditions found in the lineage comprising *Amiurus, Noturus, Prietella, Pylodictis* and *Satan*. This similarity between *Trogloglanis* and these other ictalurids could well be a synapomorphy.

(7) Lack or poor development of muscle scars on the hyomandibular (Figure 23).

(8) Separation of the facial canal and mandibularis foramen (Figure 23) could result from retarded development of bone near these foramina. However, in large, epigean catfishes, primitively these foramina are separated so this feature could also be interpreted as primitive in *Trogloglanis*.

(9) Lack of an endopterygoid ossification (Figure 23). Failure of this ossification center in *Trogloglanis* might be related to revision of upper jaw and palatine structure and not simple paedo-

morphosis. The bone is retained in some ictalurids that are as small as *Trogloglanis.*

(10) Lack of sutures between bones of the hyoid apparatus, and small hypohyals (Figure 29F).

(11) Low vertebral count. Lindsey (1975) has demonstrated a correlation between vertebral count and maximum body size in fishes.

(12) Incompletely ossified transscapular ligament. Note, however, that this structure is not fully ossified in large *Pylodictis.*

(13) Lack of the posterolateral process of the pelvic girdle (Figure 40A).

(14) Lack of pelvic splint. The pelvic splint is absent in many large catfishes also (Figure 40A).

III. Among ictalurid catfishes the uniquely derived character states of *Trogloglanis* are as follows.

(1) Keel-like structure of the segments of the body lateral line canal (Figure 1). This is also a paedomorphic feature since it must result from a failure of the post-otic lateralis placodes to sink inward during embryogeny.

(2) Presence of "coarse cilia" or the scattered club-shaped cutaneous sense organs.

(3) Extreme width of the head.

(4) Extremely narrow anterior third of the skull (Figure 6). This includes reduced margins of the frontals and absence of the dermal part of the lateral ethmoid (see II, 2 above); absence of lateral wings of the vomer, narrow supraethmoid neck, and short anterior cranial frontanelle.

(5) Funnel-shaped, permanently-open mouth, surrounded by wide, plicate lips (Figure 2B). The osteological basis for the odd mouth includes: the much shortened and elevated, transverse mandible, perforated premaxillae mounted on widely divergent ethmoid cornua, and edentulous jaw bones (Figures 6, 7, 21A, 22A–C).

(6) Hyoid arch modification related to specialized mouth architecture: deep, transverse hyoid bar, united gill membranes and obsolescent gular fold (Figures 2, 29F).

(7) Palatine bone much reduced in length posterior to its lateral ethmoid articulation (see also II, 9) (Figure 21A,B).

(8) Reduced parietal branch of the supraorbital sensory canal (Figure 6).

(9) Eight infraorbital sensory canal pores.

(10) Irregular shape of the posterior cranial fontanelle (Figure 6).

(11) Absence of laterosensory part of the posttemporal bone (Figure 6).

(12) Reduced posterior limbs of the transverse process of the complex Weberian centrum; especially in combination with robust development of anterior limbs of that process and the neural spine.

(13) Absence of primary hypurapophysis (Figure 32).

IV. *Trogloglanis* retains two relatively primitive conditions, which are shared only with the subgenus *Ictalurus*. These character states do carry some phyletic information. This is not positive evidence favoring any particular cladistic theory. But, these shared, primitive character states argue against a cladistically advanced position of *Trogloglanis* among ictalurids, i.e. a position far removed from the subgenus *Ictalurus*. This is so because the characters involved changed early in the history of the large sister lineage of *Ictalurus*, comprised of *Amiurus, Noturus, Prietella, Pylodictis* and *Satan*.

(1) The interopercle bone is expanded posteroventrally (Figure 23).

(2) The supraneural and nuchal plates at the dorsal fin base are robust and superficial (Figure 32B).

V. The blocks of derived character states shared between *Trogloglanis* and various subgroups of the Ictaluridae remain to be reviewed. Three main taxa are involved: all extant ictalurids (treated here under V); the lineage comprised of *Amiurus, Noturus, Prietella, Pylodictis* and *Satan* (Section VI below), and the lineage comprised of *Noturus, Prietella, Pylodictis* and *Satan* (Section VII below).

There is one major advanced feature shared by all living ictalurids to the exclusion of the extinct genera *Astephus* and *Hypsidoris*. This is the frontal bone position of the branching of the infraorbital and supraorbital canals (Figures 6, 8–12, 15–18). This feature indicates a common ancestor for *Trogloglanis* and its extant confamilials in which jaw adductor muscle origin had shifted onto the skull roof burying the margins of the sphenotic bone. *Astephus* and *Hypsidoris* lack muscle origin on the skull roof, and the infraorbital canal exits through the sphenotic. Secondarily, *Trogloglanis* has reduced jaw adductors, but the forward shift of the sensory canal bifurcation remains fixed in the frontal bone and provides evidence for descent from an extensively muscled ancestor.

VI. *Trogloglanis* shares at least five derived features with the monophyletic group comprised of *Amiurus, Noturus, Prietella, Pylodictis* and *Satan*.

(1) There is no contact between the supraoccipital spine and supraneural. The primitive aspect of the supraneural bone in *Trogloglanis* was mentioned above. Nevertheless, failure of the supraoccipital spine to touch the supraneural is derived relative to conditions in *Ictalurus puntatus* and *I. furcatus*. Separation of these bones is moderate in *Trogloglanis* and most species of *Amiurus*, whereas it is extreme in *Noturus, Prietella, Pylodictis* and *Satan*. We know that this character state can evolve in parallel, however, because contact of the bones is broken in some members of the subgenus *Ictalurus* (e.g., *I. lupus, I. dugesi, I. pricei*).

(2) The caudal fin is emarginate, truncate or round in shape.

The exceptional *I. (Amiurus) catus* has been mentioned earlier, but the lobed tail of this species appears to be an evolutionary reversal.

(3) The proximal pectoral spine dentations are attached to the dorsal half of the spine shaft.

(4) The upper limb of preopercle is reduced (fragmented or or lost). This feature of *Trogloglanis* was listed under Section II above as possibly resulting from small size. Accordingly it should be viewed as equivocal evidence for the relationships being discussed here.

(5) The lateral ethmoid wing is reduced (short or the dermal part lost). Like 4, this feature was mentioned under Section II as a paedomorphic condition, and it should receive low weight.

It will be recalled that *Amiurus, Noturus, Prietella, Pylodictis* and *Satan* hold other derived features in common (see page 00) which are not also shared by *Trogloglanis*. These derived features evolved after the lineage leading to *Trogloglanis* split off. In other words, *Trogloglanis* as the sister group of *Amiurus, Noturus, Prietella, Pylodictis* and *Satan*, simply retained some primitive conditions which were not left unmodified in the ancestor of its sister group. This hypothesis most easily explains how *Trogloglanis* held onto the primitive conditions listed in Section IV above.

VII. *Trogloglanis* also shares some advanced features with the group comprised of *Noturus, Prietella, Pylodictis* and *Satan. Amiurus* is not included here. These derived character states are some, but not all, of those listed on page 00 above as evidence for the monophyletic state of *Noturus, Prietella, Pylodictis* and *Satan*.

(1) The sphenotic bone does not extend anteriorly beyond the level of the epiphyseal bar.

(2) The dorsal edge of the adductor crest on the hyo-mandibular is below the level of the opercular facet.

(3) The posterior cleithral process is very short.

(4) The transscapular ligament is incompletely ossified.

Of these characters the last was mentioned in Section II above as possibly due to small body size. Alone these character states suggest that *Trogloglanis* is the sister group of *Noturus, Prietella, Pylodictis* and *Satan*. This hypothesis, however, appears less parsimonious than that discussed in Section VI for the following reason. If *Trogloglanis* is the sister group of *Noturus, Prietella, Pylodictis* and *Satan* it should possess at least all of the derived states (or more) that *Amiurus* shares with *Noturus, Prietella, Pylodictis* and *Satan*. As noted under VI, *Trogloglanis* does not possess all of these. And, reviewing list IV, *Trogloglanis* is definitely primitive relative to these taxa in a number of ways.

Based on the foregoing I conclude that *Trogloglanis* is a member of the assemblage of extant ictalurid genera; it is not a relict of some otherwise extinct early Tertiary lineage. *Trogloglanis* does not bear a

sister group relationship to any single ictalurid taxon of generic or subgeneric rank. *Trogloglanis* is likely the sister group of the major lineage comprised of *Amiurus, Noturus, Prietella, Pylodictis* and *Satan* (Figure 3). If this is correct, *Trogloglanis* diverged from its sister group before many recognizable shared derived conditions could evolve. And, although uniquely derived in many features, *Trogloglanis* has retained some relatively primitive conditions.

DATING THE ORIGIN OF TROGLOGLANIS.—The time of origin of *Trogloglanis* (or the divergence of its ancestor from other ictalurids) is an important, though difficult, historical question. Longley and Karnei (1978) exhaustively describe the known localities of capture of *Trogloglanis* and *Satan*. These fishes have been taken only from artesian wells over 305 meters deep in the vicinity of San Antonio, Bexar County, Texas. They believe these fishes to be restricted to the San Antonio pool of the aquifer in the Edwards Limestone Formation. Collecting efforts elsewhere in the region have not yielded catfishes whereas cave aquatic invertebrates have been found. The cave fish probably originated at or near this place.

The interstitial freshwater systems are in the Edwards Formation limestone of Cretaceous age. Their development commenced with regional uplift, entrenchment of streams and karst formation. Exposed limestone caves in the region have relatively young sediments; the earliest mammal fossils from caves are early or middle Pleistocene in age (Lundelius and Slaughter, 1971). Lundelius and Slaughter note, however, that Cretaceous deposits are known from caves in Wise County, and undated subsurface paleokarsts are prominent in the Texas karst regions (Smith, 1971). The geologic and hydrologic evidence for dating the formation of caves on the Edwards Plateau has been reviewed thoroughly by Sweet (1978) and Potter and Sweet (1978). Sweet's evaluation favors initiation of subsurface drainages by the middle Miocene. This is more consistent than hypotheses of Pliocene or Pleistocene origins with indirect lines of evidence bearing on the age of *Trogloglanis*. Assuming that *Trogloglanis* developed *in situ*, an origin before early Eocene is highly improbable. The early Tertiary deposits of this area belong to the Midway and Wilcox groups. These are marine deposits. *Trogloglanis* and all of its ictalurid relatives are primary freshwater fishes with very low physiological tolerance for salt water. Furthermore, on the cladistic hypothesis suggested above and on paleontological grounds, it is likely that *Trogloglanis* branched off from its sister lineage in or before the Oligocene. The oldest extinct bullhead *I. (Amiurus) pectinatus* dates from the Oligocene (Lundberg, 1975a) and is, of course, a member of the supposed sister group of *Trogloglanis*. The subgenus *Ictalurus* is also known from rocks of Oligocene age (Lundberg, 1975a).

In summary, no ictalurids were in Bexar County before at least middle Eocene because of the presence of marine habitats only. The

immediate epigean ancestors of *Trogloglanis* evolved by middle Oligocene, leaving a long period of geological time for the many specializations of this lineage to develop. The advanced features adaptive to permanent life in caves could have had fifteen million years or more to evolve if the epigean ancestor entered interstitial waters soon after the habitat began to form. In contrast to the high degree of divergence of this lineage, other extant ictalurid higher taxa have been remarkably conservative. An excellent fossil record documents no major morphological change in *Ictalurus*, *Amiurus* and *Pylodictis* since middle Miocene time (Lundberg, 1975a).

With the recent discovery by Glenn Longley and his associates of much additional material of *Trogloglanis* and *Satan*, the possibilities are greatly increased for detailed comparative investigations which should provide tests of the theories put forward above.

ACKNOWLEDGMENTS

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