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BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 124 : ARTICLE 1 NEW YORK : 1962

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 124, article 1, pages 1–30, figures 1, 2, plates 1–28, table 1

Issued June 18, 1962

Price: \$1.75 a copy

INTRODUCTION

DESPITE THE FACT that many catfishes are well known to emit sounds, reports in the literature are very sparse and sporadic. Agassiz (1850) briefly discussed the fact that catfishes and other fishes grunt by forcing air out of the swim bladder through the pneumatic duct. Dufossé (1874) mentioned the sounds produced by *Silurus glanis* as being such eruptions or "*bruits de souffle*."

The squeaking or grating sound of the base of the pectoral fin spine as it rotates within its socket was described by Sørensen (1894) and by Burkenroad (1931) for a number of catfishes. In *Galeichthys* and *Bagre*, at least, such sounds have not been recorded from freely swimming animals under water, do not occur under normal circumstances, and are very unlikely to serve any communicatory function (Tavolga, 1960).

The grunting or humming sounds ascribable to the "elastic spring" mechanism were described by Sørensen (1894) for *Doras*. In this form, the sound was reported loud enough to be audible in air up to a distance of 100 feet. In addition, Sørensen demonstrated that, in the pimelodid catfish *Platystoma*, the extrinsic "compressor" muscles were responsible for sound production. Aside from some general comments on fish sounds by Aristotle, probably the earliest identified sonic catfish was *Synodontis*, reported by Geoffroy St.-Hilaire in 1829. In Egypt, this fish was commonly called "*porcus, parce que, disent les auteurs, il grogne comme le cochon*." One of the sonic catfishes, not specifically identified, was reported by Smith (1927) to be a common noisemaker in Siam. The "singing fish" of Ceylon, heard mainly at night and sounding like a distant automobile horn, was identified by Lange (1953) by its common name in Tamil, but from the account it was probably a catfish. The grunting sounds of *Galeichthys* were described by Burkenroad (1931), and the mechanism of the "elastic spring" was thought to be responsible.

Dobrin (1947) was one of the earliest investigators to record and measure under-water catfish sounds and, indeed, probably any fish sounds. The species named in his paper was *Felichthys felis*, which is now a synonym of *Bagre marinus*, but it is quite

certain that he meant the common sea catfish *Galeichthys felis*. He reported a rhythmic drumming noise, with a sound pressure of about 0.8 microbar and a fundamental frequency of around 150 cycles per second. Knudsen, Alford, and Emling (1948) reported the sea catfish as producing a "popping" or "drumming" noise. On a commercially available record, Kellogg (1955) presented a sample of sounds produced by a large chorus of thousands of individuals of *Galeichthys*. He very aptly described it as sounding like the "bubbling of a giant percolator."

In a previous report (Tavolga, 1960), the under-water sounds of both *Galeichthys* and *Bagre* were described in detail, with the aid of sound spectrograms and accompanying recordings. The descriptions are summarized below in the present paper.

This report seeks to establish the morphological basis of sound production in the ariid catfishes *Galeichthys* and *Bagre*. Both the sea catfish, *Galeichthys felis* (Linnaeus), and the gaff-topsail catfish, *Bagre marinus* (Mitchill), are common estuarine and shore-line forms in Florida, where all this work was done. The skeletal structures involved are described first, then the muscles and their innervations. In the process of determining the precise muscles and nerves responsible for sound production, I obtained data on the physiology of these structures that enabled me to form some interpretation of the mechanics of the apparatus. It can be assumed that the structure of the swim bladder and associated sonic organs determines the quality (or timbre), pitch, and other properties of the sounds that are emitted (Fish, 1954; Tavolga, 1960), but the exact acoustics of the sound-producing mechanisms have not yet been satisfactorily explained, nor has the reason for the high efficiency of these low-frequency, under-water loud speakers.

ACKNOWLEDGMENTS

The research for this paper was supported by a contract between the Office of Naval Research, Department of the Navy, and the American Museum of Natural History, Contract No. Nonr 552 (06) NR 301-322.

The author is greatly indebted to Mr. F. G.

Wood, Jr., Director of Exhibits at Marine Studios, St. Augustine, Florida, for making the facilities of the Marineland Research Laboratory available for this project. Mr. Clifford Townsend and the entire Collecting Department of Marine Studios were extremely helpful in obtaining the fish used in this work.

The assistance of Mr. G. Scott Johnson, presently at Indiana University, is gratefully acknowledged. Mr. Johnson was a participant in the Undergraduate Research Training Program of the National Science Foundation, sponsored by the American Museum of Natural History.

The author is also grateful for the comments and criticisms of Dr. Lester R. Aronson and Dr. Bobb Schaeffer, of the American Museum of Natural History.

KEY TO SYMBOLS AND ABBREVIATIONS ON THE PLATES

aort. can., aortal canal formed by the overgrowth of a superficial layer of ossification covering the ventral and lateral surfaces of the first several vertebral centra
aort. grv., aortal groove (as above)
ART, articular
BOC, basioccipital
CENTR-1, first vertebral centrum
CENTR-6, sixth vertebral centrum
Cer. hemi., cerebral hemisphere (frontal lobe)
CERHY, ceratohyal
CLEITH, cleithrum
COR, coracoid
DENT, dentary
DETH, dermethmoid
DSOC, dermosupraoccipital
EPHY, epihyal
EPOT, epiotic
EPOT-LAM, epiotic lamina
EXOC, exoccipital
EXOC-Col, short column of bone connecting the exoccipital with the base of the horizontal support of the Müllerian ramus
Fac. lobe, facial lobe of medulla
FR, frontal
horiz. supp., horizontal support along the anterior edge of the Müllerian ramus shown in plates 11 and 19
HYOM, hyomandibular
HYPHY, hypohyal
inc. oss., areas of incomplete ossification in the expanded fourth transverse process
IOP, interopercular
lat. supp., lateral supporting lamina of the fourth

neural spine in *Bagre* (pl. 18)
MPTER, metapterygoid
MüR, Müllerian ramus; the distal end of the anterior ramus of the fourth transverse process
N. VII, facial nerve (VII)
N. IX, glossopharyngeal nerve (IX)
N. X, vagus nerve (X)
NAS, nasal
NS4, neural spine of fourth vertebra
nuch. sh., nuchal shield
Occip. n. gang., dorsal root ganglion of occipital nerve
Occip. n. dors. branch, dorsal branch of occipital nerve (to protractor muscle)
Olf. lobe, olfactory lobe
Olf. tract, olfactory tract
OPERC, opercular
Opt. lobe, optic lobe
Opt. n., optic nerve (II)
ORSP, orbitosphenoid
PAL, palatine
PASP, parasphenoid
pect. sp., enlarged first pectoral fin spine
PFR, prefrontal
PMAX, premaxillary
POP, preopercular
PROT, pro-otic
Protractor mus., protractor muscle of *Springfeder-apparat*
PT, posttemporal (supracleithrum of some authors)
PT-Inf, inferior limb of posttemporal
PT-Sup, superior limb of posttemporal
PTOT, pterotic
PTSP, pterosphenoid (alisphenoid of some authors)
PVOM, prevomer
QUAD, quadrate
Ramus recur. VII, ramus recurrens branch of facial nerve (VII)
SCB, scalebone (posttemporal of some authors)
SOC, supraoccipital
Spin. n. 1, 2, 3, spinal nerves 1, 2, and 3
SPOT, sphenotic
subv. proc., subvertebral process formed at the point of juncture of the basioccipital and the anteriormost vertebrae
sup. oss., superficial layer of ossification covering the ventral and lateral portions of the first several vertebrae
TP4, transverse process of the fourth vertebra; in the plates this label points to the terminus of the posterior ramus
TP5, TP6, TP7, transverse processes of the fifth, sixth, and seventh vertebrae
TRIP, tripus; the first and largest of the series of Weberian ossicles
URHY, urohyal
Vag. lobe, vagal lobe of medulla

SKELETAL BASIS OF SOUND PRODUCTION

IN SKELETAL STRUCTURE, and other features as well, the Suborder Siluroidea (of Regan, 1911; or Nematognathi of Jordan, 1923) is a very distinct group of fishes. The Order Ostariophysi (Cypriniformes of Berg, 1947), which includes the cyprinoids, characinoids, and gymnotoids, as well as the siluroids, is also a clear and natural group characterized by the presence of the Weberian apparatus. This series of four ossicles, which connect the cavity of the swim bladder with that of the inner ear, was first described by Weber in 1820. He named three of the ossicles "malleus," "incus," and "stapes." The fourth and innermost was called the "claustrum." To avoid erroneous implications of homology, Bridge and Haddon (1889) first proposed the terms "tripus" (instead of malleus) for the largest, crescent-shaped element; "scaphium" (instead of stapes) for the usually spoon-shaped inner ossicle that overlies the lateral surface of the sinus impar; and "intercalarium" (instead of incus) for the small ossification in the ligament between the tripus and scaphium. "Claustrum" remained as the term for the bone on the median side of the sinus impar, between it and the neural canal. The bilobed sinus impar is a posterior extension of the perilymphatic cavity. The ossicles themselves are derived from portions of the neural arches and transverse processes of the first three vertebrae, and their precise embryonic origins are still a matter of some dispute (De Beer, 1937; Krumholtz, 1943).

Weber originally postulated that the ossicles served a function of transmitting sound to the inner ear in a manner analogous to that of the middle ear ossicles of mammals. Dijkgraaf (1949, 1952, 1960) has clearly shown the broader frequency response and lower auditory threshold of ostariophysine fishes, as opposed to those that lack a Weberian apparatus. Similar data were reported by von Frisch (1923), Stetter (1929), and Evans (1925, 1935). By means of extirpation methods, von Frisch and Stetter (1932), von Frisch (1936), and Poggendorf (1952) were able to prove the auditory function of the ossicles, which does not imply, however, that the Weberian apparatus is exclusively audi-

tory in function (see reviews by Jones and Marshall, 1953, and Jones, 1957).

The skeletal characteristics of the catfishes (Siluroidea) include a non-protractile mouth with a reduced maxillary, a heavy broad cranial roof, and the ankylosis of the first several vertebrae to the occiput. The centra of the first four vertebrae are usually fused into a heavy complex, rigidly attached to the basioccipital. The fifth, sixth, and seventh vertebrae are more typical but are usually immovably joined to the first four. The dermo-supraoccipital is extended caudad and participates in the support of the nuchal shields and enlarged first dorsal fin spine. The Weberian apparatus varies from that of other Ostariophysi in the elimination of the claustrum from the functional chain of ossicles and the reduction in size of the intercalarium (Chranilov, 1929; Krumholtz, 1943).

The modifications of the fourth vertebra are of particular interest here, because the transverse processes are enlarged and invariably form the support for much of the swim bladder, and, in some forms, are associated with sound production. Bridge and Haddon (1893) described the skeletal and swim-bladder structure for most of the siluroid genera, although their arrangement of families and genera does not fit the later systematic schemata of Regan (1911) and Berg (1947). The primitive condition with respect to skeletal support of the swim bladder seems to be exemplified best by the Siluridae and the Bagridae. In these families, the large swim bladder is supported dorsomedially by the enlarged and fused centra of the first five vertebrae, dorsolaterally by a flattened shelf of bone formed by the transverse processes (parapophyses) of the fourth and fifth vertebrae, and anteriorly by a decurved extension of the anterior ramus of the parapophysis of the fourth vertebra. The latter firmly abuts the inferior limb of the posttemporal bone. Essentially, the same structure is also present in the siluroid families Plotosidae, Ameiuridae, and Chacidae, and in some members of the Schilbeidae (Bridge and Haddon, 1893; Wright, 1884; Kindred, 1919).

Johannes Müller (1842, 1843) described a

special modification of the anterior ramus of the fourth vertebra. In the genera *Auchenipterus*, *Doras*, *Euanemus* (Doradidae), *Synodontis* (Synodontidae), and *Malapterurus* (Malapteruridae), he found that this ramus was free of attachment to the posttemporal, distally enlarged into a plate attached to the forward wall of the swim bladder, and supported by a thin, spring-like parapophysis. He also found that the presence of this *Springfederapparat* was associated with a pair of protractor muscles which originate on the occipital region and insert on the anterior surfaces of the enlarged rami. He theorized that the function of this complex was to control air pressure within the swim bladder, in keeping with the Cartesian diver theory of swim-bladder function as proposed by Borelli in 1680 and originating with Robert Boyle in 1675. Bridge and Haddon (1893) described the "elastic spring" apparatus in a number of additional genera and species and added the genus *Pangasius* (family Pangasiidae) to the list. They agreed fundamentally with Müller's hypothesis of the function of this structure. Sørensen (1894) presented strong evidence that, in the Doradidae, at least, the elastic spring acted as a sound-producing mechanism, an hypothesis with which Bridge and Haddon (1894) later concurred.

The anterior ramus of the fourth vertebra shows considerable significant variations which are important in family distinctions. Its modification into a *Springfederapparat* is also quite variable, as is its "elasticity." Considering the systematic and functional importance of this structure, I propose that, regardless of its shape and function, the anterior ramus of the transverse process of the fourth vertebra in siluroids be named the "Müllerian ramus." This term also has the values of brevity and historical interest.

Many of the siluroid families possess variously specialized swim bladders of transverse tubular, bilobed, or bipartite shapes. In most of these the Müllerian rami, and in some cases other bony elements, form a pair of investing capsules of cylindrical or globular shape around the greatly reduced swim bladder. This type of modification is present in the genus *Ageniosus* of the family Doradidae (family Ageniosidae, according to Berg, 1947), in some genera and species of the

Schilbeidae and Pimelodidae, and in all members of the Amblycepidae, Sisoridae, Clariidae, Hypophthalmidae, Trichomycteridae, Bunocephalidae, Callichthyidae, and Loricariidae. In no case in which the bladder is so reduced is the Müllerian ramus modified into an elastic spring or has sound production by means of the swim bladder ever been reported.

An interesting modification is present in many species of the Pimelodidae. Members of this family that possess a large swim bladder have a Müllerian ramus of the silurid or bagrid type, in which it is firmly joined to the posttemporal, and there is no "elastic spring." Bridge and Haddon (1893) described a pair of compressor muscles originating from the occiput and inserting on the anteroventral surface of the swim bladder. They also described a pair of small muscles that always accompany the compressors. Each of these originates medially on the occiput and inserts on the tripus. They hypothesized that the tensor tripodes muscles function as dampers on the tripus against too violent air movements within the bladder. Such movements would be produced by the compressors. Sørensen (1894) clearly demonstrated, in the genus *Platystoma*, that the compressors do not compress the bladder but function in sound production. Bridge and Haddon (1894) subsequently concurred with Sørensen.

The family Ariidae is usually placed in a primitive phylogenetic status (Regan, 1911; Berg, 1947) because of the supposed fossil antiquity of the genus *Arius*. The hind part of the skull and the vertebral complex were described in detail by Bridge and Haddon (1893) for *Arius*, and other genera were briefly mentioned. The skull of *Arius* was described by Koschkaroff (1905) and figured by Gregory (1933). Karandiker and Masurkar (1954) reported on the skull of *Arius platystomus* in some detail, but did not mention the vertebral complex. Merriman (1940) figured and described some selected aspects of the osteology of *Galeichthys felis* and *Bagre marinus*. The Müllerian ramus was not described in any case, nor was its significance as a *Springfederapparat* recognized.

At this point, a nomenclatorial digression seems to be in order. It may be confusing to the reader, as it was initially to me, to have a

catfish family called Bagridae and the genus *Bagre* in the family Ariidae. The name *Bagre* Cuvier was listed as preoccupying the names *Felichthys* Swainson and *Ailurichthys* (emended to *Aelurichthys*) Baird by Jordan in 1917. *Bagre* was adopted by Hubbs (1936) and most subsequent authors. The genus *Bagrus* Valenciennes, however, is the type of the family Bagridae. It was therefore suggested by Jordan and by Hubbs that the names *Bagre* and *Bagrus*, because of their similarity, be considered homonyms and that the next available name for *Bagrus* be substituted. This would be *Porcus* Geoffroy St.-Hilaire, which would make the family name Porcidae. Jayaram (1956) interpreted the International Rules as permitting both *Bagre* and *Bagrus* to remain, the former in the family Ariidae and the latter in the Bagridae. To add complication, some authors, including Jayaram, refer to the Ariidae as the Tachysuridae.

Prior to a description of the ariid skulls, it is appropriate to give a detailed account of the condition as found in the Siluridae. The following descriptions are limited in scope to the occipital region of the skull and the anterior vertebral complex.

The nomenclature of the bones described here and labeled in the plates is based mainly on that used by Harrington (1955) and, to some extent, that of Gregory (1933).

Wallago sp.

Plates 1-3

This account is based on a specimen in the collection of the American Museum of Natural History. The skull lacks a few elements, such as a Weberian apparatus on the left side, and has a few cracked bones, but it is otherwise in good condition. *Wallago* is a member of the Siluridae, and its general cranial osteology closely resembles that of most silurids and bagrids (Bridge and Haddon, 1893; Joseph, 1960).

SUPRAOCCIPITAL

Plates 1, 3

Dorsally the dermal part of this bone is broad and slightly humped in the middle, and its surface is prominently ridged with parallel and interlacing rugosities, as is the entire dorsal cranial surface. Anteriorly it is sutured to the frontals; laterally, to the sphenotics,

pterotics, and scalebones (parietals are absent, as in all siluroids). Posteriorly the dermosupraoccipital extends as a stout process that is involved in the support of the nuchal shields characteristic of the order. Under the posterior process a median vertical supporting ridge expands at the occiput, where it sutures with the epiotics laterally and exoccipitals ventrally (pl. 3). Under the base of the posterior process is a pair of large foramina. The nerves that pass through these apertures are the rami lateralis accessorius of the facial (VII) (Herrick, 1901), also called the rami recurrens (Berkelbach van der Sprenkel, 1915, and most subsequent reports). This pair of large cutaneous sensory branches is common to siluroids. The enlarged neural spine of the third vertebra projects into a median groove on the ventral posterior surface of the supraoccipital.

EXOCCIPITAL

Plates 2, 3

A posterior, vertical ridge divides this bone into two wings. The anterolateral wing is sutured to the basioccipital, pro-otic, sphenotic, and epiotic, and it possesses a large, multiple foramen for the glossopharyngeal, vagus, and occipital nerves. The posterior, median wing is sutured to the basioccipital, epiotic, supraoccipital, and contralateral exoccipital. It forms the arch of the foramen magnum and possesses several nerve and nutrient foramina at its base. The vertical ridge extends dorsad onto the epiotic and ventrad to the base of the inferior limb of the posttemporal.

BASIOCCIPITAL

Plate 2

This bone shows few special modifications from that of the normal teleost. It is sutured to the parasphenoid, pro-otics, exoccipitals, and inferior limbs of the posttemporals. It forms the floor of the foramen magnum and possesses a small, median, nutrient foramen on its posterior ventral surface.

EPIOTIC

Plates 1, 3

The vertical ridge of the exoccipital continues dorsad onto the epiotic to form an acute angular ridge projecting caudad. Dor-

sally the epiotic is joined to the superior limb of the posttemporal; laterally it is sutured to the pterotic, medially to the supraoccipital, and ventrally to the exoccipital. A large dorsolateral foramen is present.

POSTTEMPORAL

Plates 1-3

This is the supracleithrum of Regan (1911) and others. The superior limb of this V-shaped bone is immovably joined to the scalebone (posttemporal of Regan, 1911) dorsally and the epiotic ventrally. This limb is also supported by a ventral process of the pterotic, and it fits into a fossa formed by the three supporting bones. The inferior limb of the posttemporal is columnar and firmly sutured to the basioccipital and ventral edge of the exoccipital. The distal, apical portion of the posttemporal is broadened and possesses a deep notch into which the dorsal point of the cleithrum fits. This joint is a loose one and permits some anterior and posterior swinging of the pectoral girdle, as well as some vertical sliding movement. The posterior surface of this apex has a facet at which it is firmly laced with connective tissue to the Müllerian ramus (see below).

WEBERIAN APPARATUS

A detailed account of these ossicles is not given here, for they vary little among the siluroids and are not an important element involved in sound production. Bridge and Haddon (1893) described the ossicles for most of the siluroids, and mentioned them in *Wallago* briefly. A number of more recent and detailed reports concerning these ossicles include those by Krumholz (1943) and Chranilov (1929). These structures appear to be relatively conservative, and among the various siluroid families there is little difference from the form described originally in *Silurus* by Weber (1820).

FIRST VERTEBRA

Plate 2

Only a thin centrum is present and distinguishable. Laterally and ventrally it is fused with the following vertebral complex. Midventrally an aortal groove continues caudad.

SECOND AND THIRD VERTEBRAE

The centra of these vertebrae are indistinguishably fused with the centrum of the fourth vertebra. A pair of small, lateral, wing-like projections extend from what is probably the second centrum. These serve to support, in part, the anterior wall of the swim bladder. Dorsally the arch and spine of the third vertebra project forward. The broadly compressed spine fits immovably into a groove in the supraoccipital. Posteriorly this spine joins that of the fourth vertebra by means of a thin, median lamina.

FOURTH VERTEBRA

Plates 1-3

This structure is highly modified, characteristically so in the siluroids, and it forms an important support for the anterior chamber of the swim bladder, the Weberian apparatus, and the spine of the dorsal fin. The centrum is elongate and not distinguishable from that of the fifth. It is invested by a layer of superficial bone (pl. 2, sup. oss.) which extends ventrally to form a deep aortal groove (pl. 2) along the ventral midline. The neural spine is large and inclined caudad (pls. 1, 3). It is grooved posteriorly and receives the bony supports for the spine of the dorsal fin. Anteriorly the neural spine is connected to that of the third vertebra by a median lamina. Laterally a pair of strengthening ridges extend out onto the transverse processes.

The transverse process (parapophysis) is greatly expanded and flattened to form the roof of the anterior chamber of the swim bladder (pls. 1-3). The anterior, Müllerian ramus is stout, sharply decurved, and expanded distally into a thick, rugose wing which is firmly laced to the distal end of the inferior limb of the posttemporal. The decurved portion of the Müllerian ramus supports the anterior face of the swim bladder. The posterior ramus is broad, slightly arched, inflexible, and continuous with the Müllerian ramus. Distally it fans out and is immovably joined to the parapophysis of the fifth vertebra.

FIFTH VERTEBRA

Because of the layer of superficial ossification, the fifth centrum is not distinguishable

from the fourth. The neural spine is a low, median ridge. Anterior and posterior rami of the parapophysis are visible as thickenings at the base of the transverse process. Distally the two rami fuse to a point (pls. 1-3). The sixth and following vertebrae show no special modifications.

Galeichthys felis

Plates 4, 5; 6, figure 1; 7-12

The skull and vertebral complex show few modifications from the typical ariid form as described by Bridge and Haddon (1893) for *Arius pidada*, Koschkaroff (1905) for *Arius thalassinus*, Bhimacher (1933) for *Arius* and related forms, Gregory (1933) for *Arius* sp., and Karandikar and Masurekar (1954) for *Arius platystomus*. The following description is based on several specimens of various sizes collected in the vicinity of Marineland, Florida.

SUPRAOCCIPITAL

Plates 4; 6, figure 1

Dorsally the dermosupraoccipital is a broad, rough-surfaced shield, sutured to the frontals, sphenotics, pterotics, and scale-bones. Posteriorly a broad, flat process supports the nuchal plates. The posterior face is sutured laterally to the epiotics, ventrolaterally to the exoccipitals, and medially to the neural spine of the third vertebra. On this posterior face, immediately below the projecting posterior process, is a pair of ramus recurrens (VII) foramina.

EXOCCIPITAL

Plates 5, 11

This bone is smoothly convex, unlike that of *Wallago*. It is sutured to the basioccipital, pro-otic, sphenotic, epiotic, and contralateral exoccipital, where it forms the arch of the foramen magnum. Along its ventral edge are three foramina. The middle and largest of these is for the passage of the glossopharyngeal and vagus nerves. The ventral branch of the occipital nerve passes through the posterior of these foramina. An extension from the posterior ventromedial angle of the exoccipital forms a bony column which is immovably fused to the base of the Müllerian ramus (pl. 11). A small foramen just dorsal to

this column is for the passage of the dorsal branch of the occipital nerve.

BASIOCCIPITAL

Plates 5; 6, figure 1

As in *Wallago*, the basioccipital is sutured to the parasphenoid, pro-otics, exoccipitals, and inferior limbs of the posttemporals and forms the floor of the foramen magnum. Posteriorly it is indistinguishably fused with the anterior vertebral complex of centra and possesses a large, midventral, aortal foramen. Posterior to this foramen is a prominent ventral projection, bifid at the tip. This projection, called the "subvertebral process" by Bridge and Haddon (1893), is composed of the basioccipital and at least the first two vertebral centra. The prominent subvertebral process is considered to be characteristic of the Ariidae.

EPIOTIC

Plates 4; 6, figure 1; 10-12

Except for a projecting lamina (see below), this bone is smoothly convex, sutured to the supraoccipital, exoccipital, and pterotic. Dorsally it forms a groove together with the scalebone for the reception of the superior limb of the posttemporal. From its dorsal edge a prominent lamina of stout, flat bone projects ventrocaudad. The epiotic lamina (erroneously considered part of the supraoccipital by Bridge and Haddon, 1893) extends to and is sutured to the dorsal ridge of the posterior ramus of the fourth vertebra (pls. 4, 12). Laterally the lamina has a caudally directed, pointed process, and medially it fuses with the base of the third neural spine (pls. 10, 11). The presence of this lamina is characteristic of the ariids (Bridge and Haddon, 1893), although Regan (1911) stated (in error) that in *Galeichthys* this structure does not reach the parapophysis. The epiotic lamina forms a roof over the Müllerian ramus and serves as the surface of origin for the "protractor" muscle (pl. 12; pl. 21, fig. 1). The Doradidae, which include many sound-producing species with a highly developed *Springfederapparat*, also possess posterior extensions of the epiotics, but they serve as supports for the nuchal plates (Regan, 1911) and do not appear to be involved in the sonic mechanisms.

POSTTEMPORAL

Plates 4, 5; 6, figure 1; 10-12

The superior limb is short, stout, and immovably joined to the pterotic, scalebone, and epiotic. In older specimens, there is often a small foramen between the portion joined to the pterotic and that which fits into the groove between the scalebone and the epiotic. The inferior limb is long and cylindrical, joined to the basioccipital. The distal apex has a deep notch, into which the dorsal spine of the cleithrum fits loosely (pls. 7, 9). There is no direct connection with the distal end of the Müllerian ramus (see below).

FIRST, SECOND, AND THIRD VERTEBRAE

The centra are indistinguishably fused to the basioccipital and participate in the subvertebral process. The neural spine of the third vertebra is shaped like an I beam, and it is inclined forward to join the base of the supraoccipital.

FOURTH VERTEBRA

The fourth, fifth, sixth, and seventh centra are fused together and covered ventrally and laterally by an investing layer of bone (pls. 5; 6, fig. 1; 11, 12). This superficial ossification forms a large, mid-ventral, aortal canal, which extends from the basioccipital to the base of the seventh vertebra (pl. 5). The presence of such a canal, rather than a groove, was considered an ariid character by Bridge and Haddon (1893).

The Müllerian ramus (pls. 4, 5; 6, fig. 1; 10-12) is decurved, pointed, and stiffened along its anterior edge by a thin horizontal ridge (pl. 11, horiz. supp.) extending from the base of the third arch. At its base it is attached by a short column to the exoccipital (pl. 11). The distal tip of the Müllerian ramus is freely movable within the limits of elasticity of the transverse process as a whole. In *Arius*, Bridge and Haddon (1893) stated that the distal tip is "applied to" the posttemporal. Gregory (1933), in his figure, showed it to be free, while Regan (1911) said that it was "rigidly attached" in the Ariidae. In all specimens that I have seen, the distal tip is only very loosely attached to the posttemporal by a small portion of areolar con-

nective tissue. In dried and partially cleaned skeletons, however, this tissue sometimes remains and hardens and resembles a ligament, which may explain the discrepancies in the accounts. Conceivably, considerable specific and generic variation may also exist. The matter is important, because the freedom of movement of the Müllerian process is an essential feature in the sound-producing mechanism. In freshly dissected specimens, the distal tip of the Müllerian ramus is movable only in a dorsoventral arc. The horizontal ridge described above prevents movement in any but the dorsoventral direction.

The *Springfederapparat* itself is a thin, fragile shelf forming an arched fan, ventrally concave, connecting the anterior and posterior rami of the fourth vertebra (pl. 12). Even in young specimens, less than 4 inches in total length, this region is thoroughly ossified, while other parts of the cranium are still partially cartilaginous. Sounds can be elicited from such individuals.

The posterior ramus is rigidly supported by the epiotic lamina (pls. 10-12). Thus a deep, roughly tetrahedral cavity is formed, bounded on three sides by the *Springfederapparat*, epiotic lamina, and lateral occipital region (epiotic and exoccipital; pl. 12). Within this cavity is the "protractor" muscle (pl. 21, fig. 1).

The fourth neural spine is formed as in *Wallago*, inclined caudad and supporting the underpinnings of the spine of the dorsal fin (pls. 6, fig. 1; 10, 12).

The divisions between the fifth and sixth and sixth and seventh vertebrae are visible from above. Each has a pair of parapophyses (pls. 4, 5). The fifth pair is the longest and broadest and is firmly joined to the posterior edge of the fourth.

Bagre marinus

Plates 6, figure 2; 13-20

The major features of the skull and other aspects that distinguish this species from *Galeichthys* were described by Merriman (1940). In the following description, the points of difference between *Galeichthys* and *Bagre* are emphasized. The account is based on several specimens collected in the vicinity of Marineland, Florida.

SUPRAOCCIPITAL

Plates 6, figure 2; 13, 18, 20

The bone is basically the same as that of *Galeichthys* and that of *Arius*, except for a mid-ventral ridge under the posterior projecting process. This ridge is fused with the neural spine of the third vertebra. The foramina of the rami recurrens (VII) are lower in position.

EXOCCIPITAL

Plate 14

A broad, thin, medial process projects back over the neural canal and meets, but does not fuse with, the third neural spine. Along the ventral edge there are a small anterior foramen and a large middle foramen (glossopharyngeal and vagus), followed by a smaller foramen for the ventral branch of the occipital nerve. Behind the last-mentioned, a short extension supports the anterior portion of the tripus. Dorsal to this extension is the foramen for the dorsal branch of the occipital nerve. The exoccipital process in *Galeichthys* which projects dorsal to the tripus and joins the base of the Müllerian ramus is represented in *Bagre* by a small point on the median edge of the exoccipital.

BASIOCCIPITAL

Plates 6, figure 2; 14

This bone is almost identical in form to that of *Galeichthys* and contributes to a prominent subvertebral process.

EPIOTIC

Plates 6, figure 2; 13, 18, 20

In basic form and in the shape of the projecting lamina, the epiotic is like that in *Galeichthys*. The lamina, however, is narrower and is not joined medially to the neural arch. The effect therefore is to reduce the surface area available for the origin of the protractor muscle.

POSTTEMPORAL

Plates 6, figure 2; 13, 14, 18-20

The superior limb is short and proximally biramous. Its anterior ramus is sutured to the pterotic, and the posterior ramus fits into a deep groove formed by the scalebone and the

epiotic. The notch at the distal apex of the posttemporal is very deep and wide. In dissections, the cleithral spine is found to fit very loosely into this notch, thus permitting vertical sliding as well as swinging movements of the pectoral girdle (pls. 15, 17). There is no connection with the Müllerian ramus.

FIRST, SECOND, AND THIRD VERTEBRAE

The neural spine of the third vertebra resembles that of *Wallago* in being compressed into a thin median ridge ankylosed to the supraoccipital. This thin ridge is continuous caudad with the fourth neural spine. The first and second vertebrae are not distinguishable.

FOURTH VERTEBRA

The Müllerian ramus is stoutly supported along its anterior edge by a horizontal shelf leading from what appears to be the base of the third arch (pls. 14, 19, 20). This structure is also present in *Galeichthys*, but in *Bagre* it is slightly less flexible. The thin, curved lamina that joins the Müllerian ramus with the posterior ramus is even more delicate and fragile than in *Galeichthys*, particularly in the region lateral to the juncture of the epiotic lamina, where the bone has lacy areas of incomplete ossification, even in mature specimens (pls. 13, 14, 19). A similar area is usually present on the dorsal, posterior surface of the *Springfederapparat*, just medial to its juncture with the epiotic lamina (pl. 19). Because of the stout horizontal support, the dorso-ventral flexibility of the *Springfederapparat* is less in *Bagre* than in *Galeichthys*. The distal tip of the Müllerian ramus is free of the posttemporal, as is probably true of most ariids.

The neural arch of the fourth vertebra is vertical (pls. 6, fig. 2; 20) and is supported laterally by a pair of flat, triangular lamina, the bases of which are fused to the posterior rami (pl. 18). A large vertical fossa is thus formed on each side of the supraoccipital process (pls. 13, 20), bounded anteriorly by the occiput, laterally by the epiotic lamina, posteriorly by the flange of the fourth spine, and ventrally by the base of the Müllerian ramus. A portion of the epaxial musculature fits into this fossa. The insertion of this muscle is the skin of the dorsum and the base of the dorsal fin.

THE MUSCULAR BASIS OF SOUND PRODUCTION

AMONG THOSE SILUROIDS that possess a *Springfederapparat* as a modification of the Müllerian ramus, there is invariably a muscle that originates on the occipital region of the skull and inserts on the anterior face of the expanded Müllerian ramus. Müller (1842, 1843) first described the presence of such a muscle in a number of genera of the families Doradidae, Synodontidae, and Malapteruriidae. Bridge and Haddon (1893) called this a "protractor" muscle and described its presence in some additional forms, including the family Pangasiidae. The exact origin of the muscle was reported as being the posterior face of the epiotic and exoccipital.

Sørensen, in his doctoral dissertation in 1884 (not seen by me), first postulated the function of the protractor muscle and the *Springfederapparat* in sound production and also presented some experimental evidence.

Ever since Sørensen's (1894) and Bridge and Haddon's (1893, 1894) reports, the sound-producing potential of the *Springfederapparat* has been recognized in all the above families. In the Ariidae, Burkenroad (1931) described the grunt-like sounds of *Galeichthys milberti* (= *G. felis*) as being produced by a mechanism similar to the "elastic spring." He reported the presence of dorso-ventrally oriented muscle fibers inserting on the thin shelf of bone over the dorsal face of the anterior swim-bladder chamber. Although his description was brief, it is now clear that he was discussing the "protractor" muscle. Despite the fact that sound production has probably been known from the first moment that a man caught a sea catfish, Burkenroad's is the earliest published account that I can locate of sound production in this family (Ariidae).

The following descriptions are based on dissections of fresh and preserved specimens, and on serial sections of juvenile individuals. The latter were fixed in 10 per cent formalin in sea water, decalcified in formic acid, sectioned at 10 microns, and stained with Delafield's hematoxylin and eosin. Small portions of the protractor muscle, with other muscles from the same individuals, were fixed in Gilson's fluid, sectioned at 2 microns, and stained

with hematoxylin and eosin. As controls, portions were taken from the levator pectoralis (trapezius), the pectoral fin adductor, and the epaxial muscle from the midbody region.

Galeichthys felis

Plates 21, figure 1; 22

In dissection, the protractor muscle can best be approached from the side. A soft, triangular area can be discerned by palpation just behind the cleithrum. The anterior, vertical leg of the triangle is formed by the posttemporal; the dorsal leg, by the outer edge of the epiotic lamina; and the ventral leg, by the outer edge of the fourth parapophysis. The last of these is not palpable from the surface, because it is deeper and thinner than the others. After the skin and superficial muscle in this region are peeled away, the triangular area occupied by the protractor is easily evident, especially in a fresh specimen. The muscle is quite visible because of its deep red color. It is obviously much more highly vascularized than any of the neighboring tissues, and indeed more so than any other muscle tissue in this fish. The protractor muscle is soft and spongy in texture, and further dissection is best continued after the muscle is hardened in fixative.

Most of the volume of the tetrahedron formed by the occiput, epiotic lamina, and Müllerian ramus is occupied by the protractor muscle (pls. 12; 21, fig. 1). Its surface of origin is an oval that extends over the entire ventral surface of the epiotic lamina, including the medial portion that unites with the third neural arch. A few bundles of fibers also originate from the portion of the epiotic proper just beneath the lamina. The almost circular area of insertion is the thin layer of bone from the ridge along the anterior edge of the Müllerian ramus to the site of fusion of the epiotic lamina with the posterior ramus, i.e., the insertion covers a large portion of the dorsal surface of the *Springfederapparat*.

The general shape of the protractor muscle is that of a greatly truncated cone. The fiber bundles from the surface of origin converge slightly as they approach the insertion surface

(pls. 21, fig. 1; 22). The anterior fibers are longest and converge most, whereas the posterior fibers are short and are almost parallel to one another. In the posterior portion, the fiber bundles extend unbroken from origin to insertion, while in the anterior portion, a few columns of fibrous tissue run from points of convergence of muscle bundles to the surface of insertion.

Sections perpendicular to the long axis of the fibers show the presence of numerous capillaries between the fibers and a central core of loose fibrous tissue and larger blood vessels. The diameter of the fiber bundles ranges from 600 to 700 microns, and the bundles are all roughly circular in cross section.

In tissues taken from mature specimens (more than 10 inches in length), fixed in Gilson's fluid, the diameter of the muscle fibers ranges from 25 to 45 microns (average about 30 microns) and the cross striations are distinct, with the sarcomere size about 1 micron. Nuclei are peripheral in position. Myofibrils are very fine, closely packed, and with relatively little sarcoplasm around them. In tissues from juveniles (less than 4 inches in length), the fibers are thinner (6 to 15 microns, average 12 microns) and the striations very sharp (p. 22, fig. 2). The sarcomeres are almost 3 microns in length, and the Q bands appear finely granular under $\times 1000$ bright-field magnification. These tissues were fixed in 10 per cent formalin in sea water, and the differences in fiber size and striations may be in part the result of a different fixative. The Gilson's fixed material is probably more reliable and in general shows fewer artifacts.

In comparison, similarly treated (Gilson's fixation) muscle tissue from other parts of the same individuals shows clearly larger fibers, with more variability in size. Diameters range from 75 to 150 microns (average about 100 microns). The striations appear less distinct, but have the same spacing, and the myofibrils are coarser, with the intervening sarcoplasm more visible.

It is well known (Prosser, 1950) that fast-acting muscles tend to have finer, more closely packed myofibrils with less sarcoplasm than slower-acting types. The so-called "dark" muscles are generally slow acting, and their color is the result of the accumulation of myoglobin in the tissue. The deep red coloration of the protractor muscle is probably caused not by myoglobin but by the high degree of vascularization. The tissue, in a freshly dissected animal, bleeds profusely when damaged even slightly, and the coloration is quickly washed out during fixation, which is not true of "dark" muscles.

Bagre marinus

Plate 21, figure 2

In dissections, the protractor muscle is more difficult to locate than is that of *Galeichthys*. The posttemporal extends laterad, and the dorsal spine of the cleithrum protrudes dorsad so as partially to cover the triangular area within which the protractor is placed (pl. 20). A considerable amount of superficial muscle and connective tissue must be removed before the protractor can be exposed. Once revealed, it can be easily seen and recognized because of its triangular shape and deep red color.

In *Bagre*, the protractor muscle is smaller than that of *Galeichthys*, and it is conical in shape (pl. 21, fig. 2). The surface of origin is an oval on the distal two-thirds of the ventral side of the epiotic lamina. All the fibers converge to a small area of insertion just median to the tip of the Müllerian ramus dorsal to its horizontal supporting ridge. The surface along which the muscle lies is always well ossified. The sites of incomplete ossification are never those involved with the attachment of the protractor.

Except for the greater convergence of fibers and additional fibrous tissue connecting these, the protractor muscle of *Bagre* is identical in microscopic anatomy to that of *Galeichthys* (see above).

NERVE SUPPLY OF THE SOUND-PRODUCING MECHANISM

THE INNERVATION of the protractor muscle is virtually the same in *Bagre* and *Galeichthys*, so that one description serves for both. Slight differences, where they occur, are mentioned. The description is based on dissections of both fresh and preserved specimens, and on serial sections of juvenile individuals. The protractor muscle is supplied entirely by a branch of the occipital nerve (nomenclature according to Addens, 1933, but see discussion below). The innervation was established not only by anatomical observations (pls. 23, 24) but by stimulation experiments.

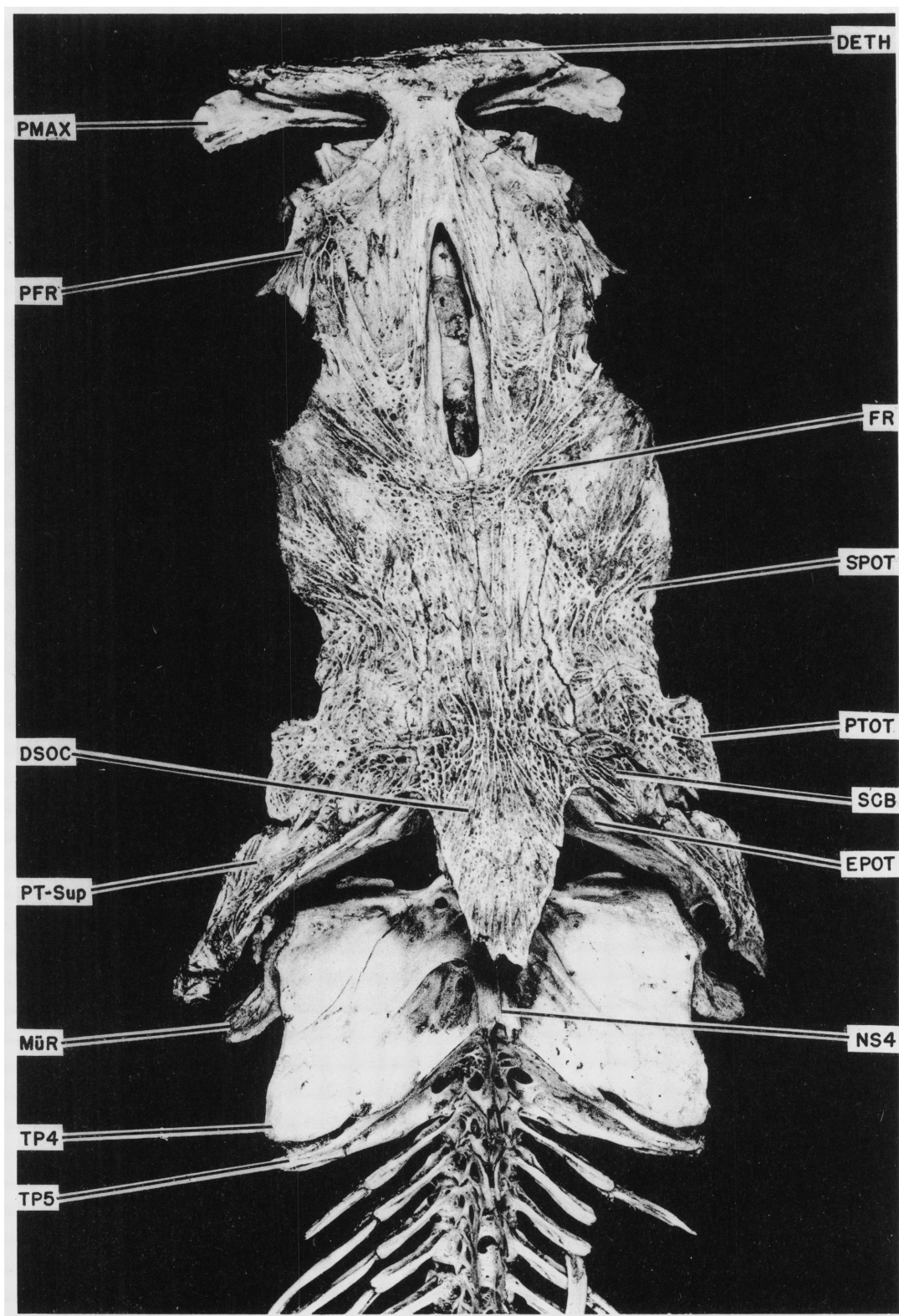
On exposure of the cranial cavity, the occipital nerve roots can be seen just posterior to the roots of the vagus (pl. 23). The occipital nerve possesses a dorsal root, with a ganglion, and a ventral root. Posteriorly the next nerve is clearly a true spinal nerve, with its roots just posterior to the foramen magnum. The occipital nerve penetrates the lateral floor of the exoccipital and emerges through two foramina posterior to the vagus-glossopharyngeal foramen. The upper of the two foramina serves the dorsal branch of the occipital nerve. The dorsal branch runs caudad along the outside of the exoccipital portion of the auditory capsule almost up to the ventral surface of the epiotic lamina. Here it turns laterad and ramifies into the protractor muscle along its surface of origin. In *Bagre*, the nerve passes through, but does not innervate, a large mass of epaxial muscle before reaching the protractor.

The course of the ventral branch of the occipital nerve is also of interest, and some ancillary problems are touched on as it is described. It is a larger nerve than the dorsal branch and presumably contains sensory as well as motor fibers. The ventral branch runs laterad and follows the anterior surface of the inferior limb of the posttemporal for about one-third of its length, then turns abruptly ventrad. At this turn, a small twig is given off laterally, along the posttemporal, to the anterior surface of the cleithrum. Here this twig ramifies into a large, oval muscle, the origin of which is the ventral surface of the pterotic and insertion on the anterior surface of the dorsal limb of the cleithrum (see pls. 7-9,

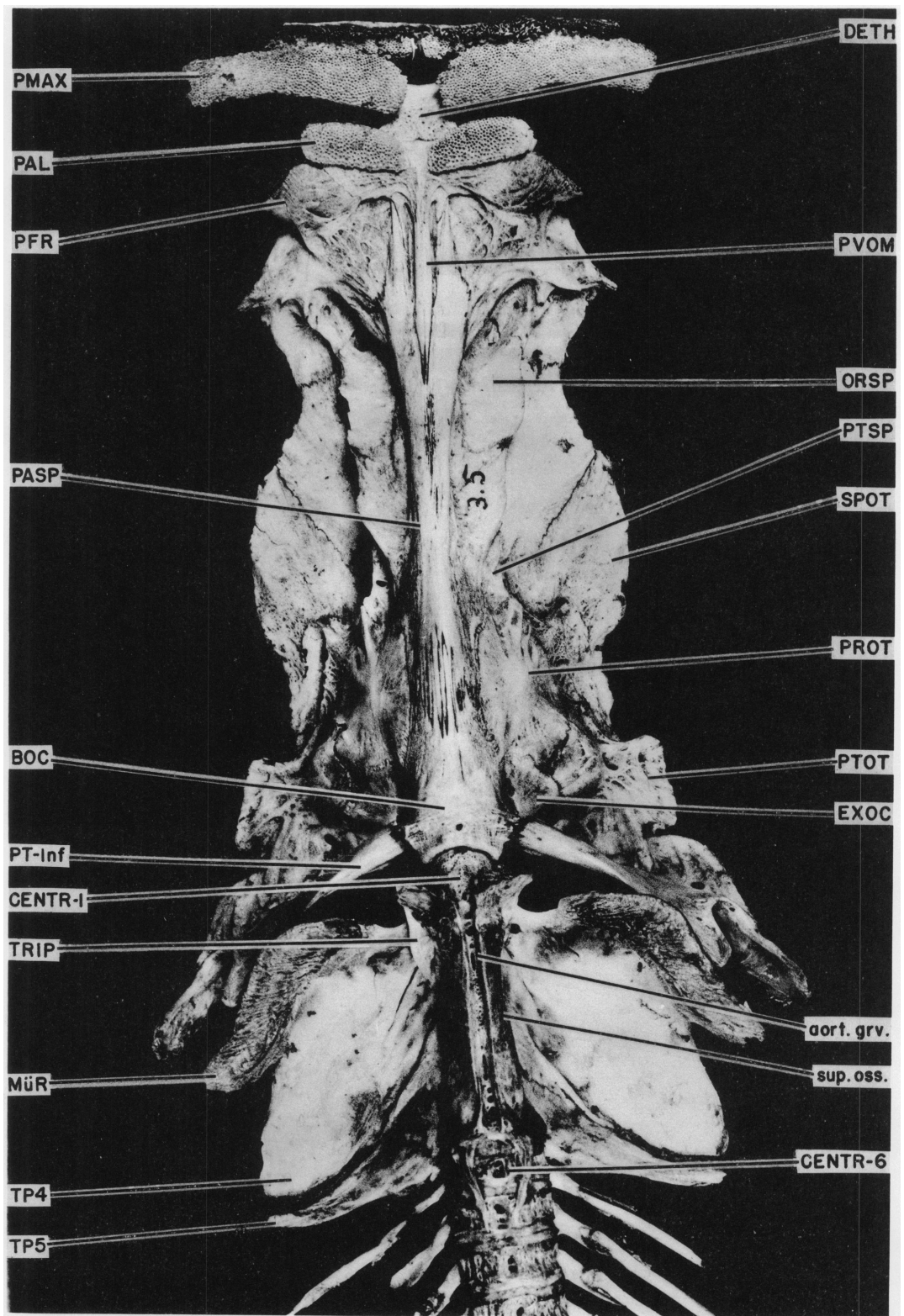
15-17 for skeletal parts). Stimulation of the muscle shows that it functions as a levator pectoralis. It is not clear, however, whether the twig of the occipital nerve is a motor nerve or not. Innervating this muscle is also a twig from the last branchial nerve (vagus). This was found in the study of serial cross sections. What is most probably the same muscle has been described in *Ameiurus* as the trapezius by McMurrich (1884). Wright (1884) stated that it was innervated by a branch of the first spinal nerve (=occipital nerve). Herrick, in his work on *Menidia* (1899) and *Ameiurus* (1901), claimed that Wright was in error and that the trapezius muscle is innervated by the posteriormost branch of the vagus, i.e., a precursor of the eleventh nerve. In the codfish, *Gadus*, Herrick (1900) located a functionally comparable muscle innervated by spinal nerves and concluded that in this form a true trapezius was absent. According to Addens (1933), the trapezius of teleosts is probably homologous to that described in selachians and ganoids. The fact of differences in innervation does not preclude common origin, according to Black (1917), and, based on embryological studies, Edgeworth (1911) concluded that the trapezius of teleosts is derived from the upper edge of the fourth levator arcuum branchialum, regardless of innervation.

Below the posttemporal, the ventral branch of the occipital nerve runs within a sheet of connective tissue that forms the septum between the pericardial and perivisceral cavities. Here the nerve splits into a lateral and a medial branch. The lateral is the larger of the two, and it joins branches from the first and second spinal nerves. Together, these nerves form a portion of the brachial plexus or ramus cervicalis. Stimulation of the occipital nerve at this point shows that it is a motor supply to the adductors and abductors of the spine of the pectoral fin.

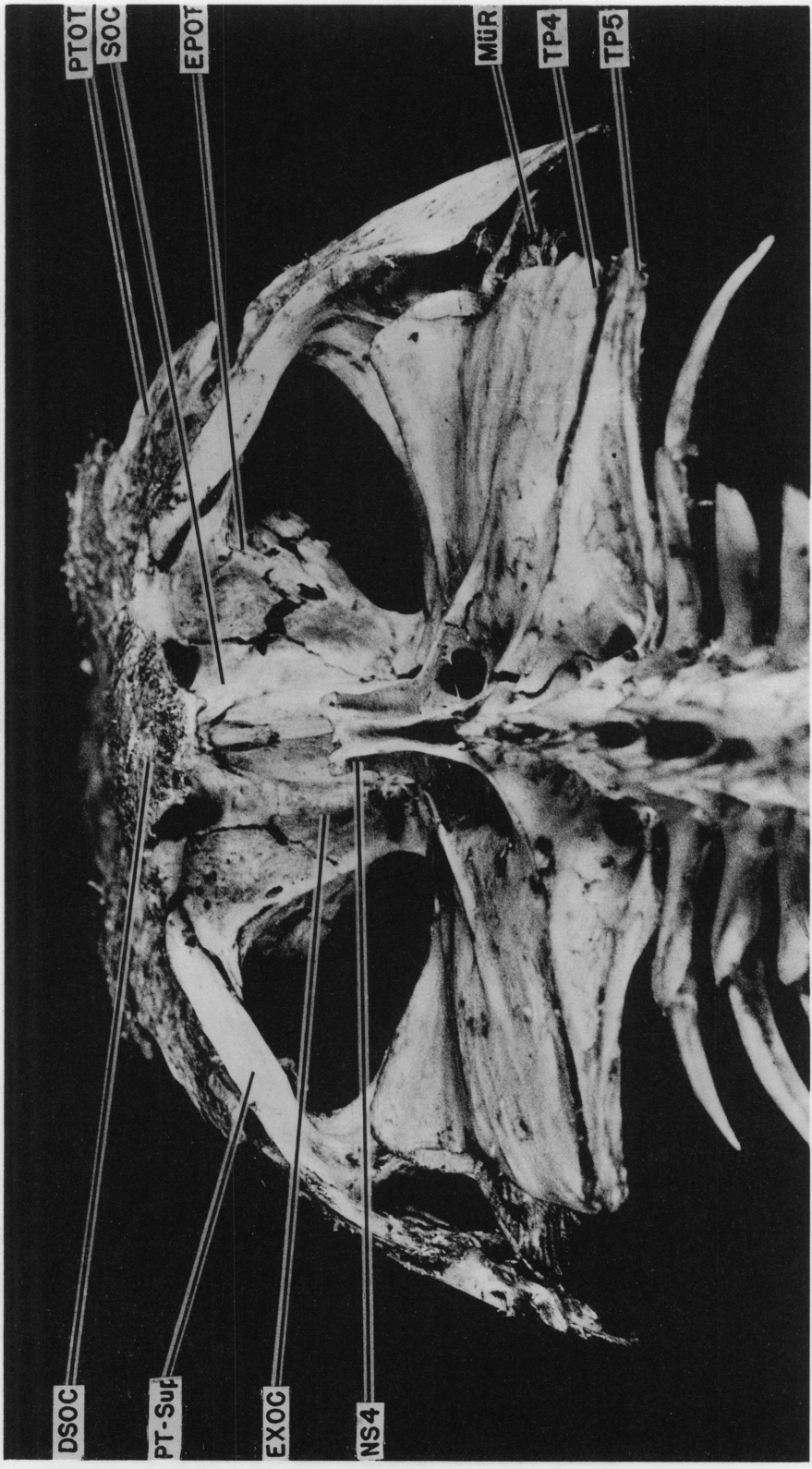
The smaller medial branch runs ventrad and forward along the dorsomedial edge of the cleithrum. As it turns forward, it sends a few short twigs to some small slips of muscle. These short muscles run from the edge of the cleithrum where it unites with the coracoid



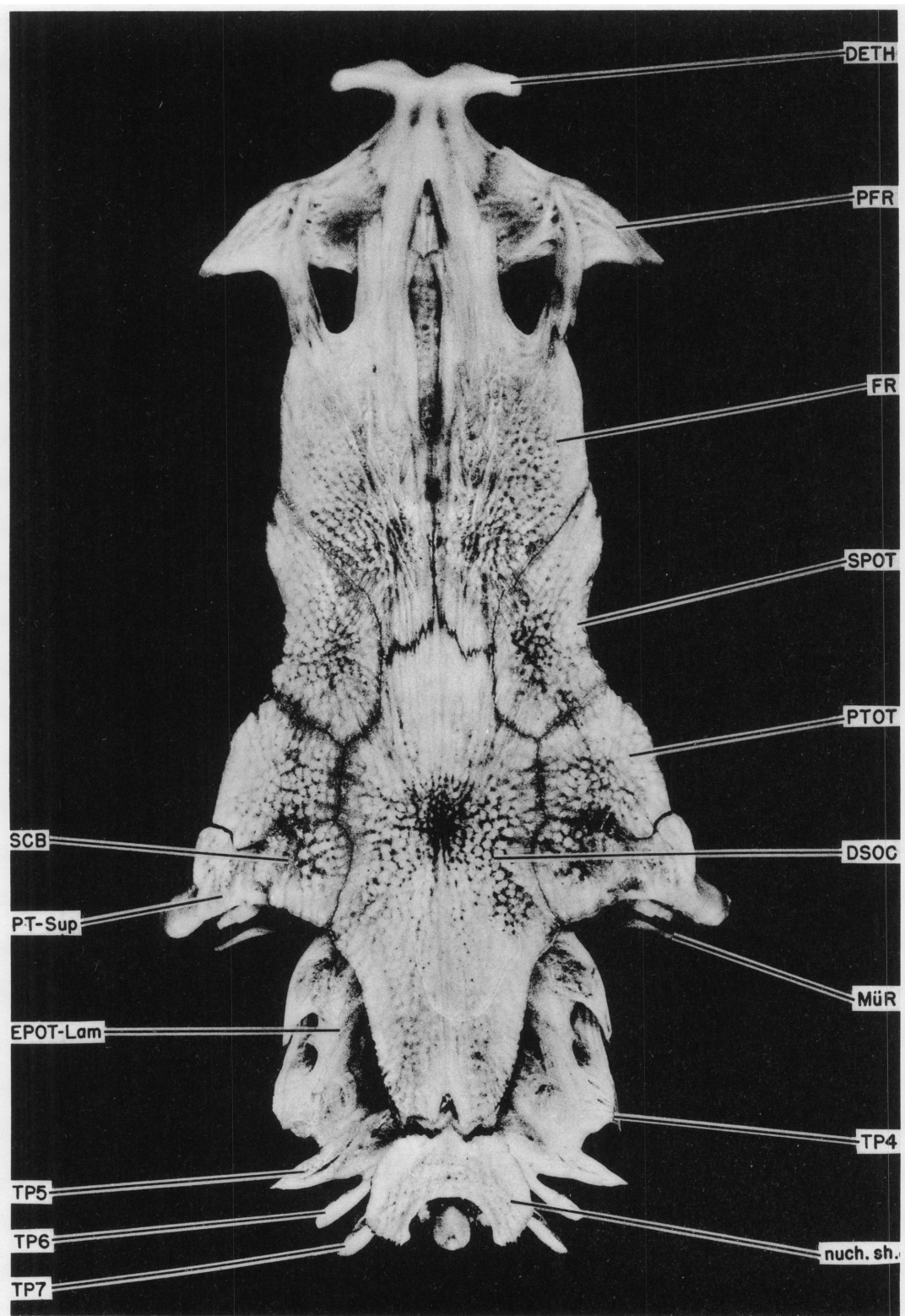
Dorsal view of neurocranium and anterior vertebral complex of *Wallago* sp. $\times \frac{1}{2}$



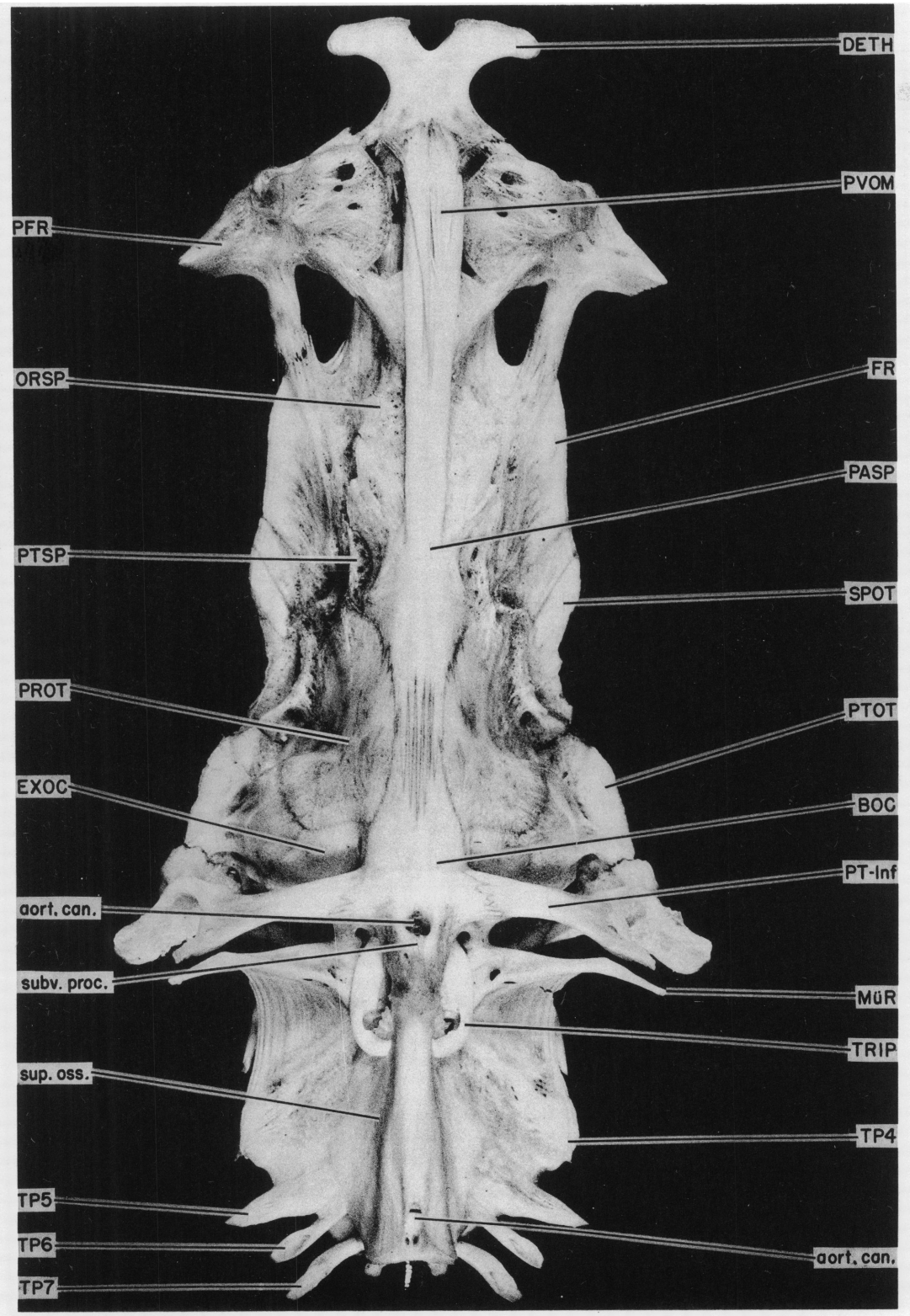
Ventral view of neurocranium and anterior vertebral complex of *Wallago* sp. $\times \frac{1}{2}$



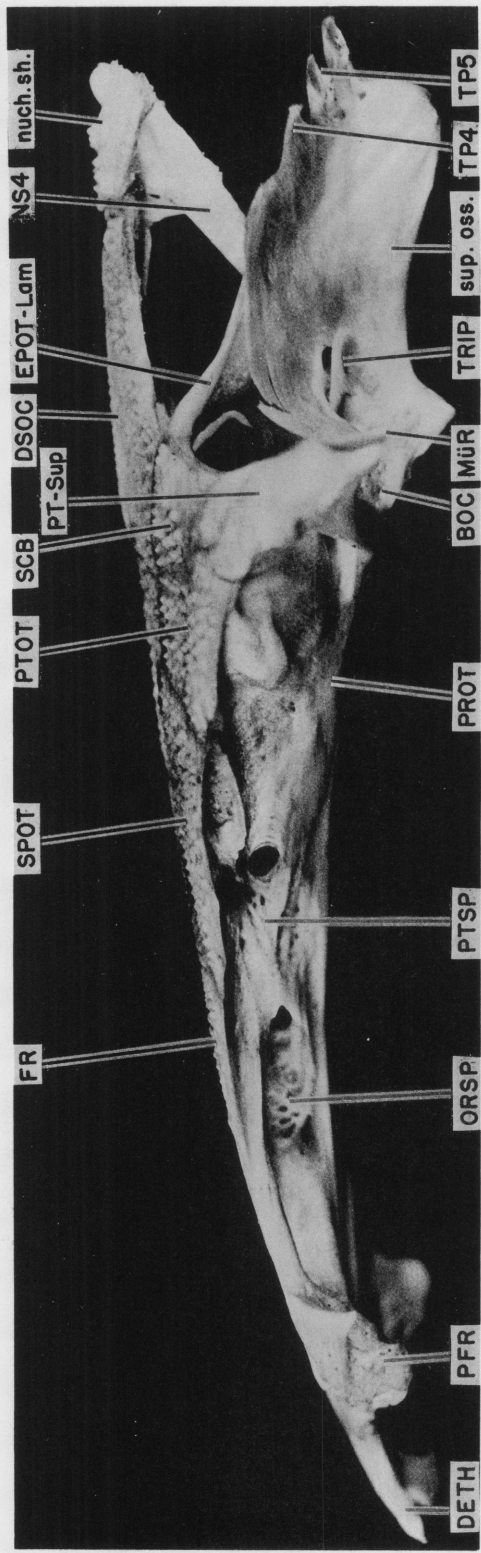
Occipital view of neurocranium and anterior vertebral complex of *Wallago* sp. X 1



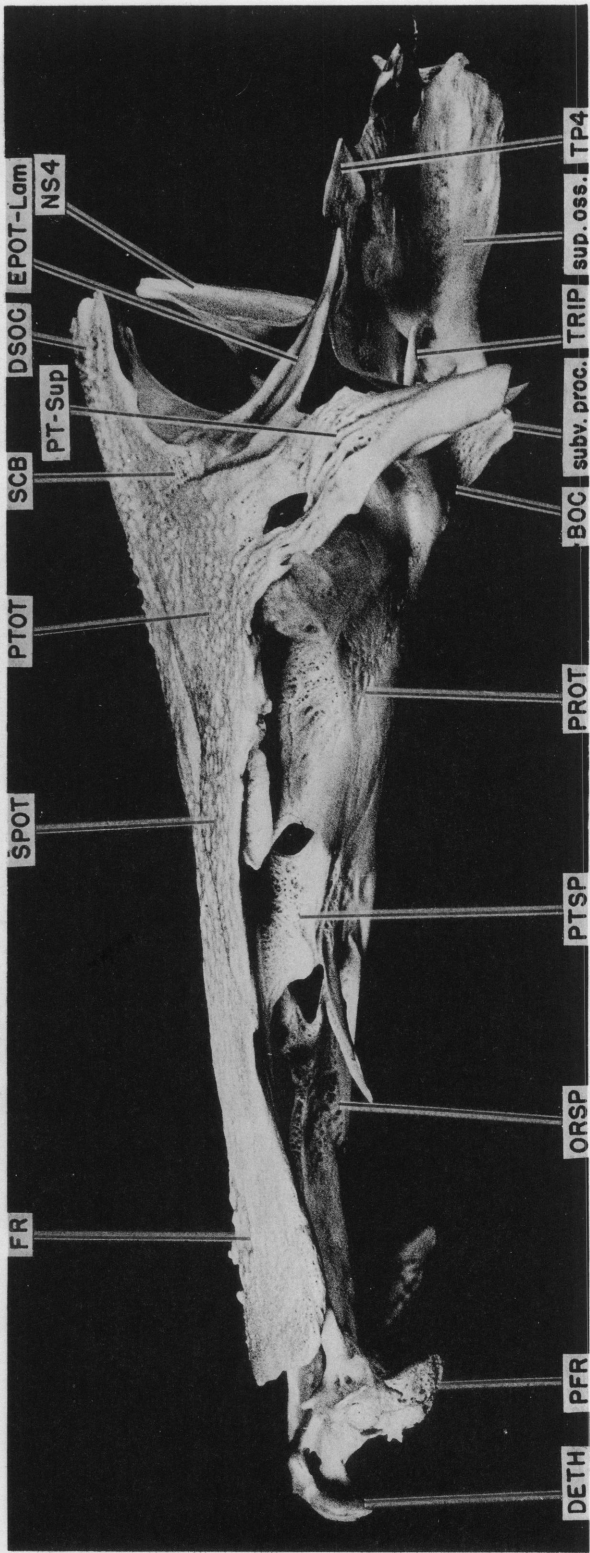
Dorsal view of neurocranium and anterior vertebral complex of *Galeichthys felis*. $\times 2$



Ventral view of neurocranium and anterior vertebral complex of *Galeichthys felis*. $\times 2$

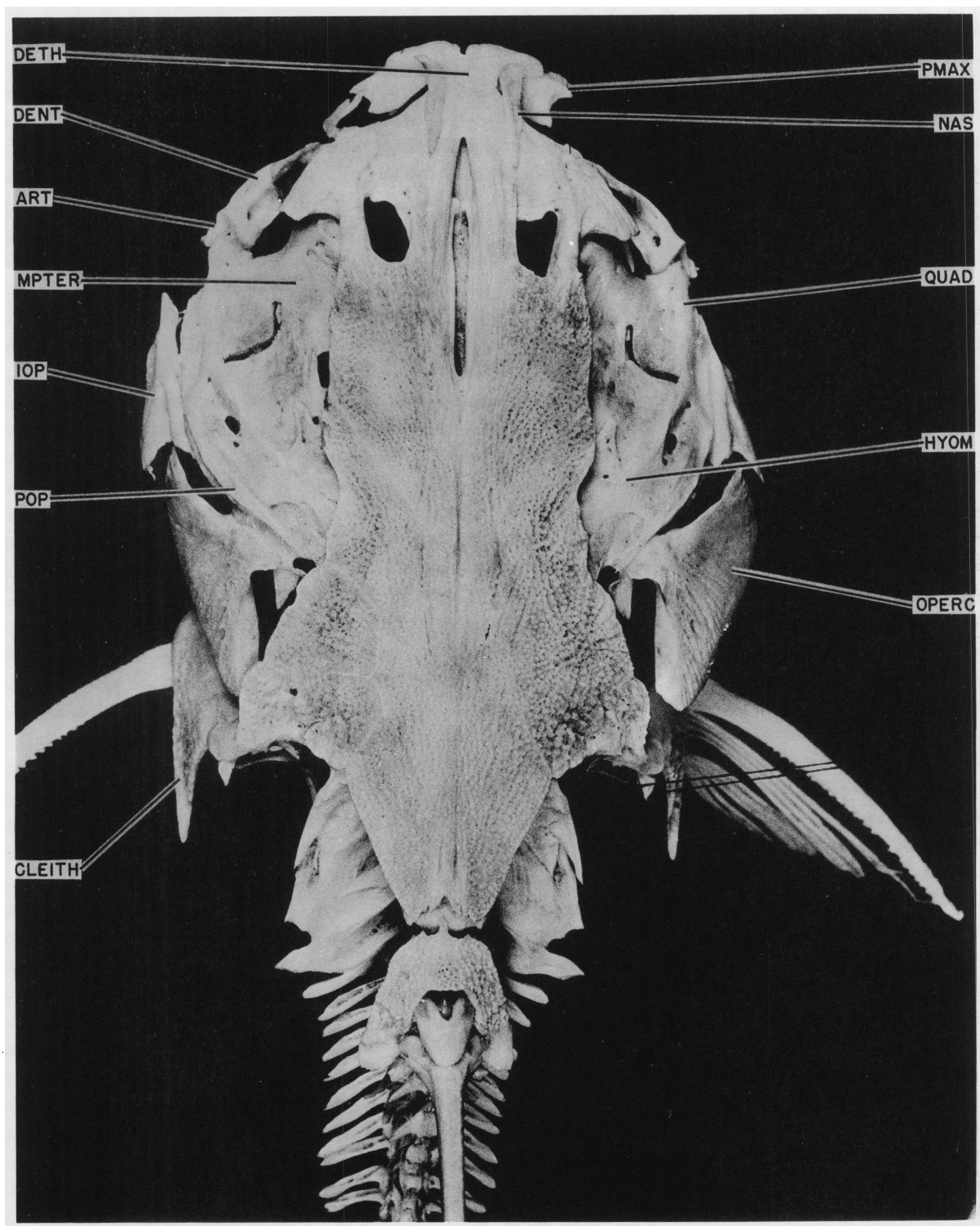


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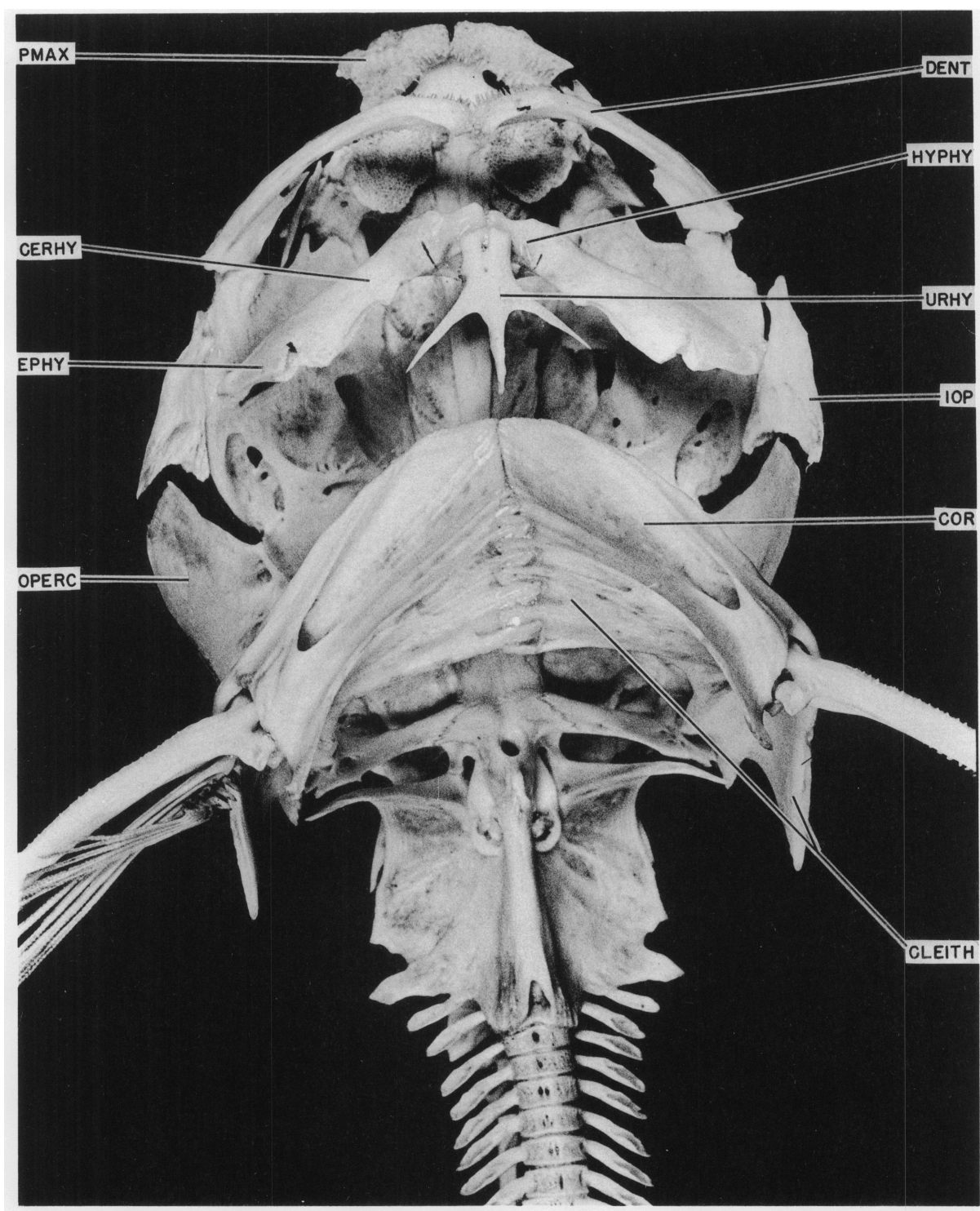


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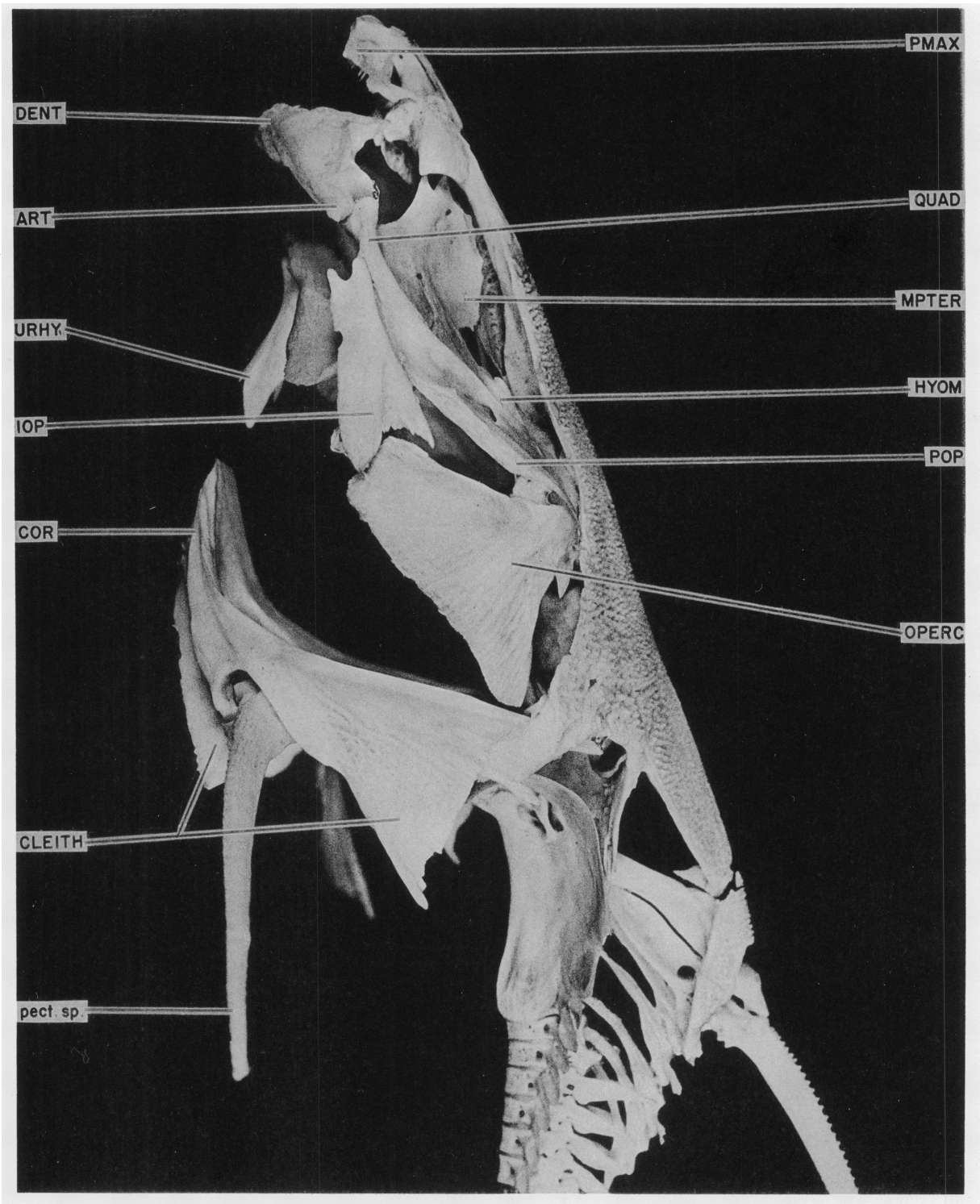
1. Left lateral view of neurocranium and anterior vertebral complex of *Galeichthys felis*. X 2
2. Left lateral view of neurocranium and anterior vertebral complex of *Bagre marinus*. X 1



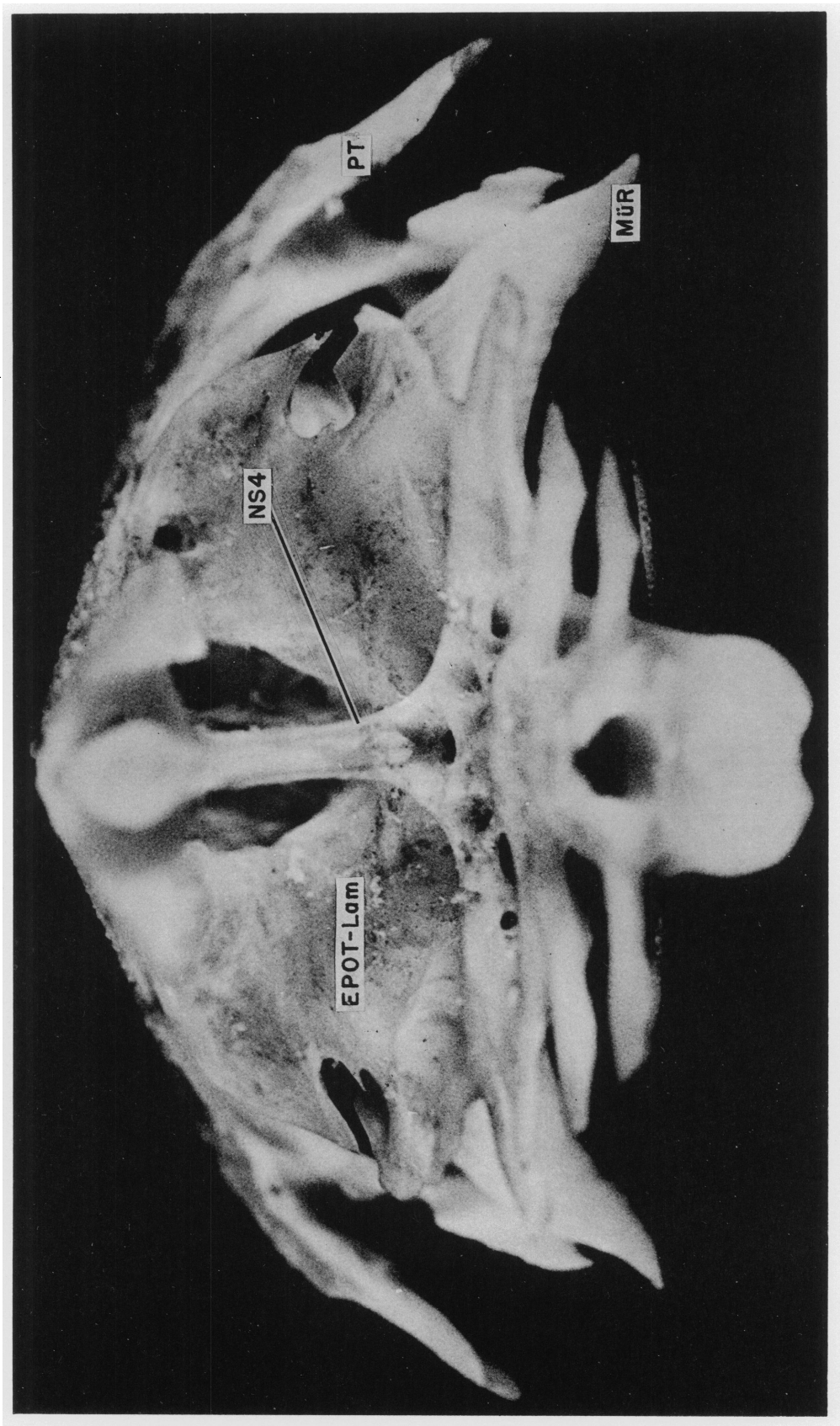
Dorsal view of cranial and pectoral skeleton of *Galeichthys felis*. $\times 1$



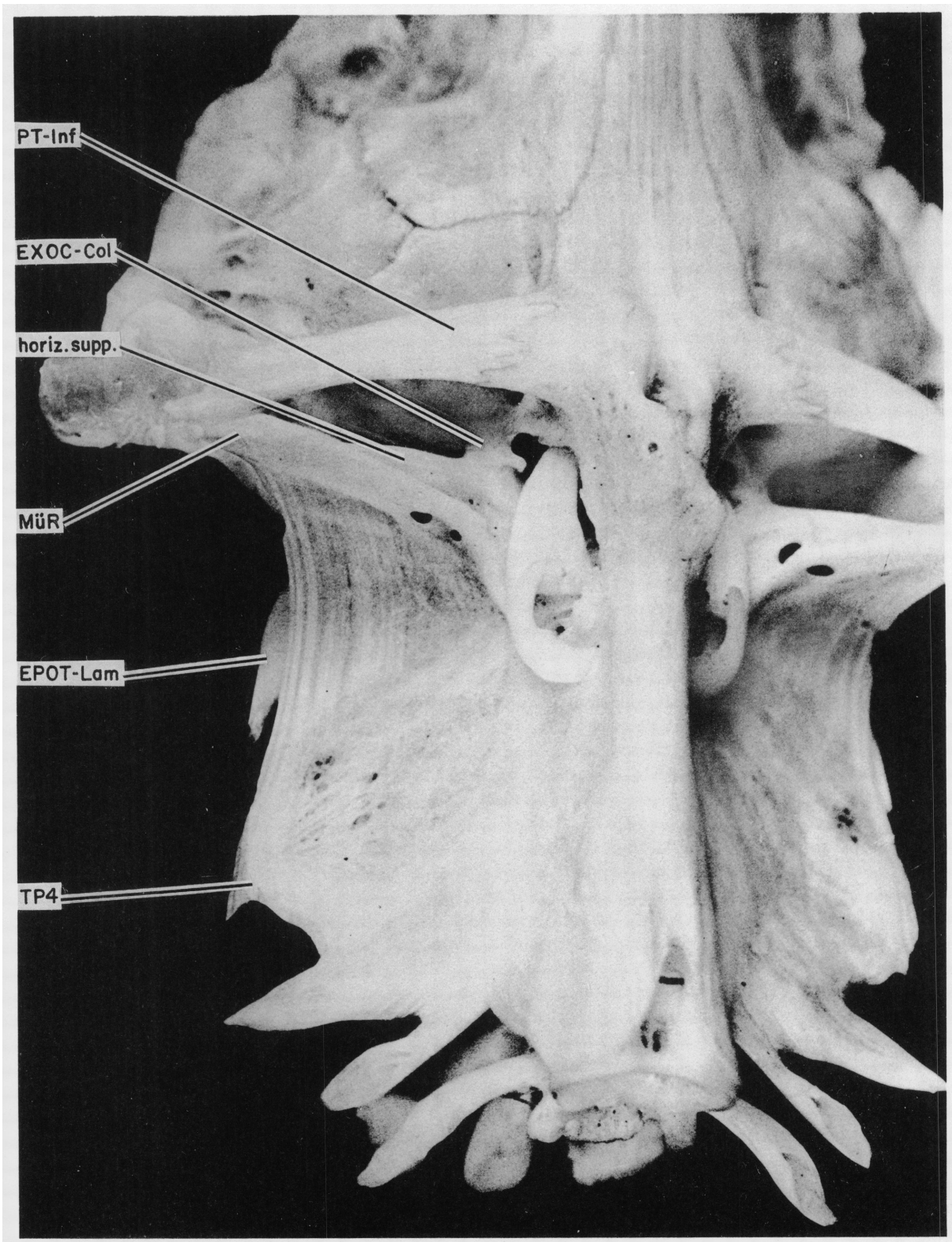
Ventral view of cranial and pectoral skeleton of *Galeichthys felis*. $\times 1$



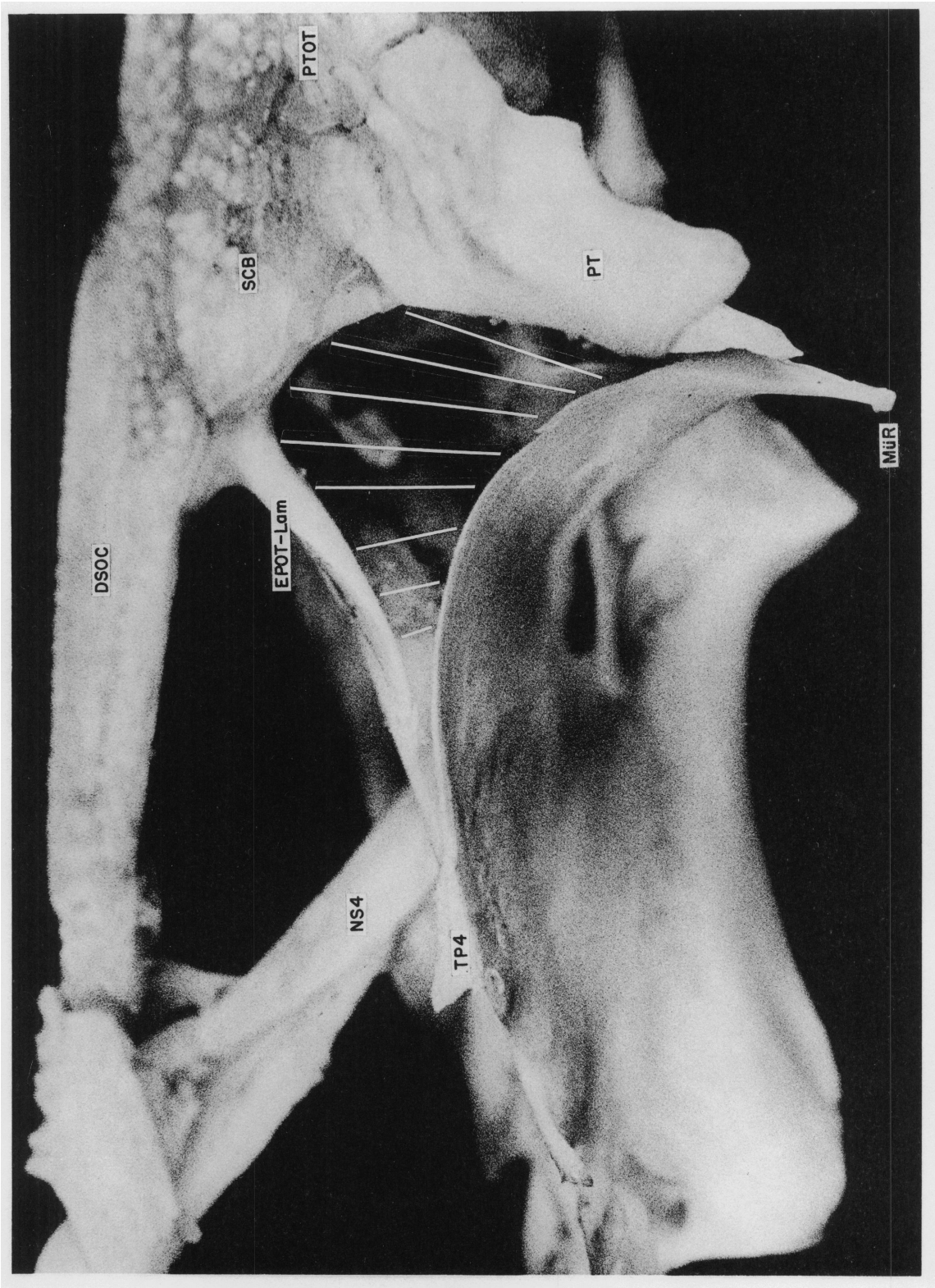
Left lateral view of cranial and pectoral skeleton of *Galeichthys felis*. $\times 1$



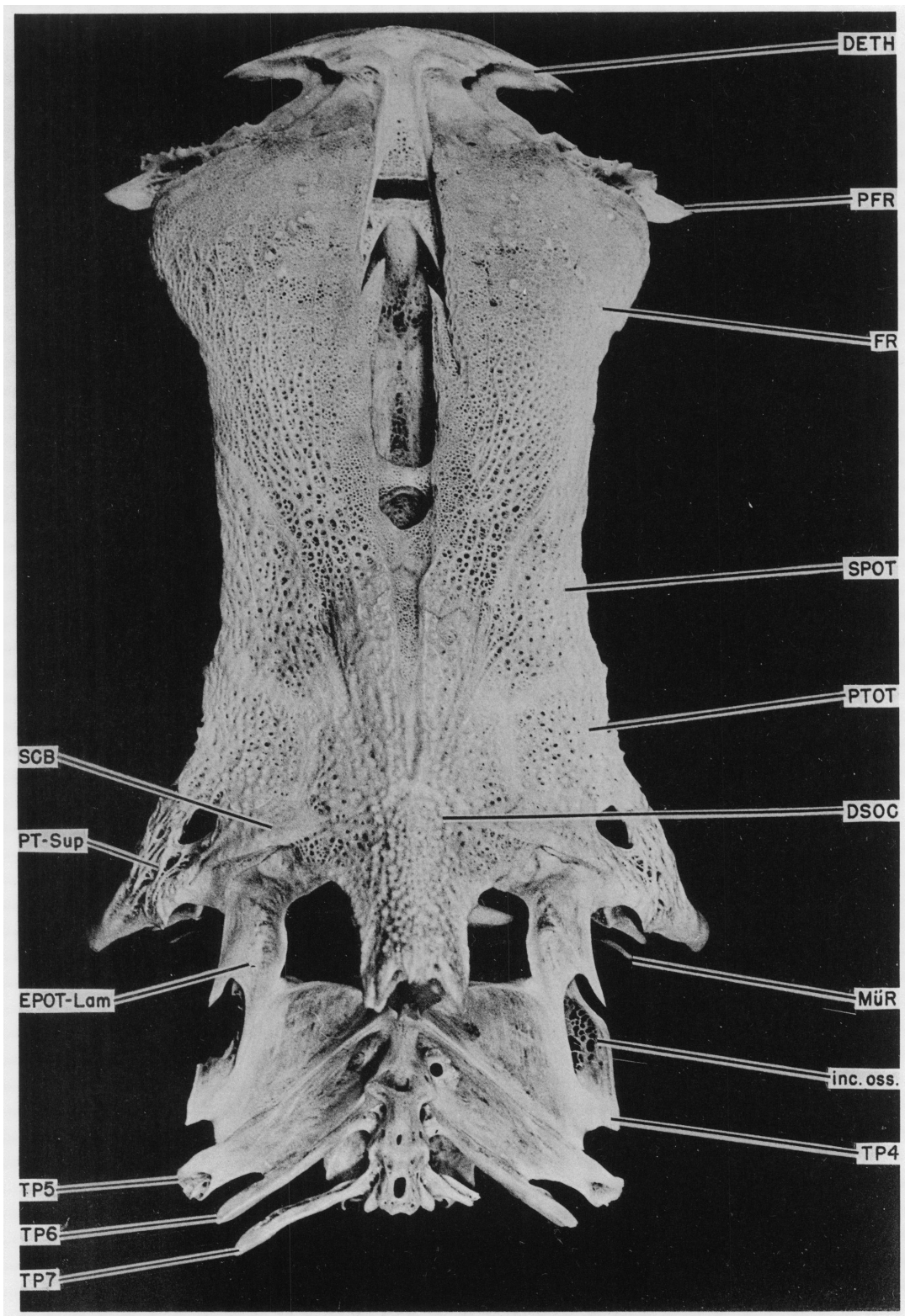
Occipital view of neurocranium and anterior vertebral complex of *Galeichthys felis*. X 4



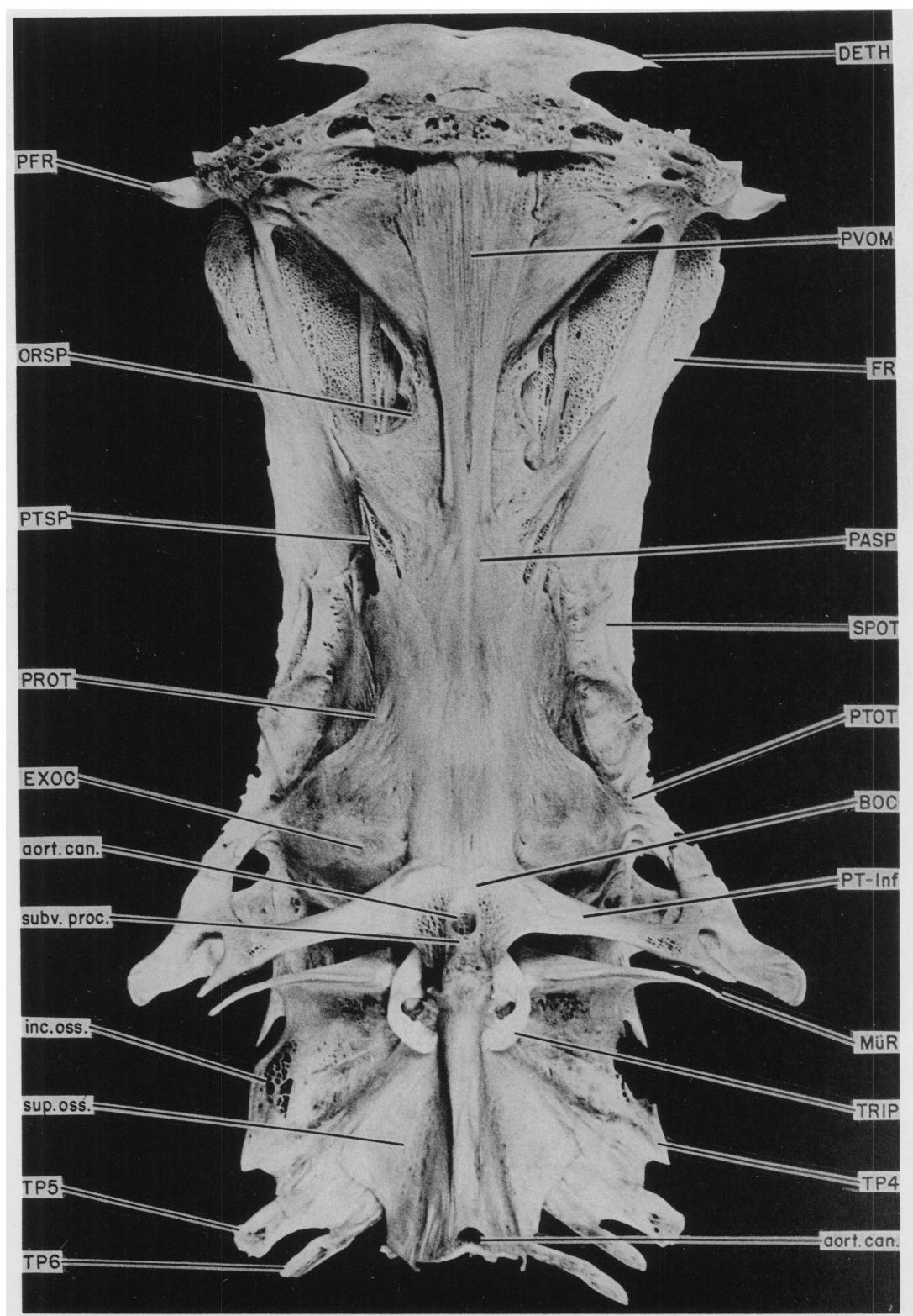
Ventral view of *Springfederapparat* and associated structures of *Galeichthys felis*. $\times 4$



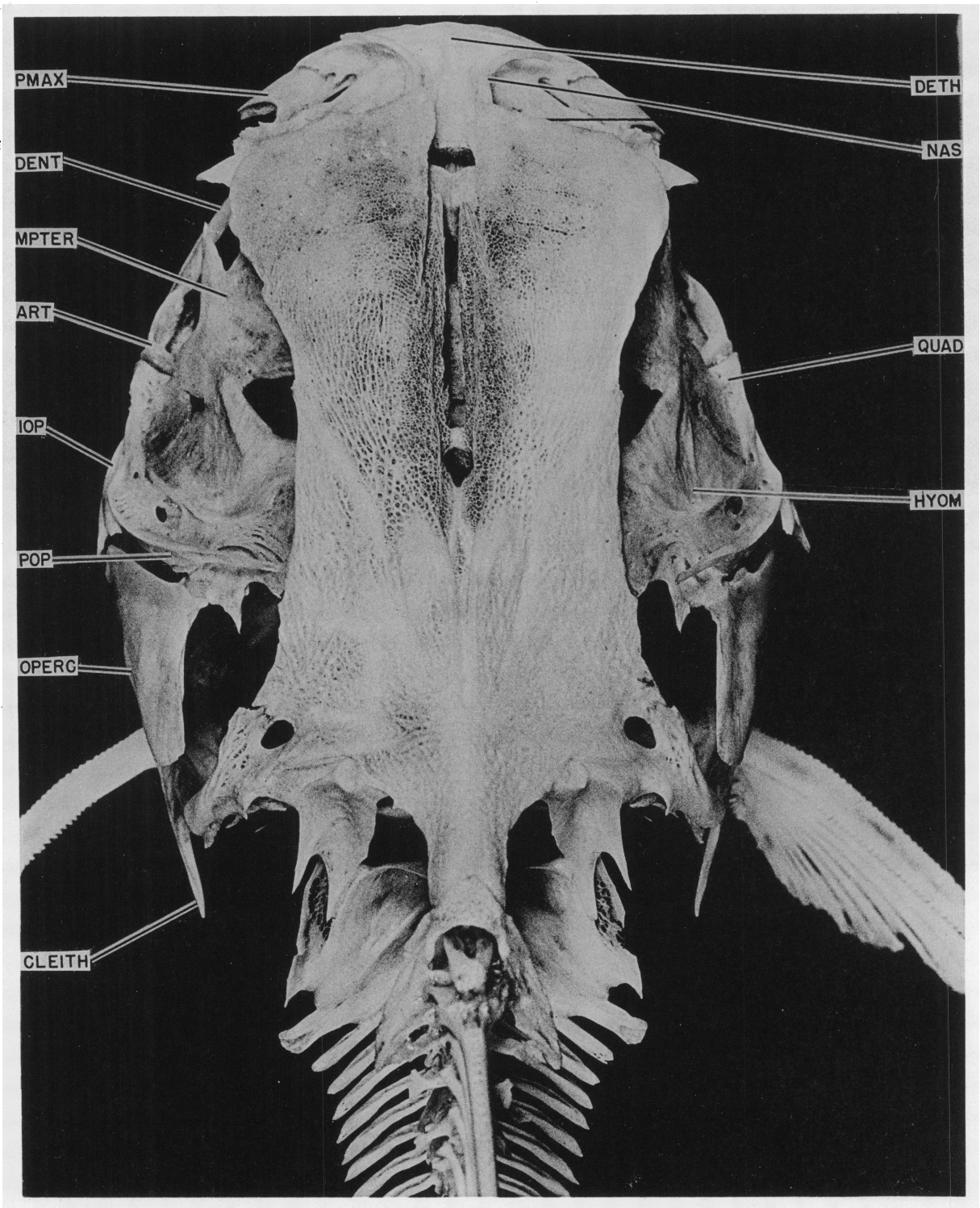
Right lateral view of *Springfederapparat* and associated structures of *Galeichthys felis*. White lines represent position of protractor muscle. $\times 6$



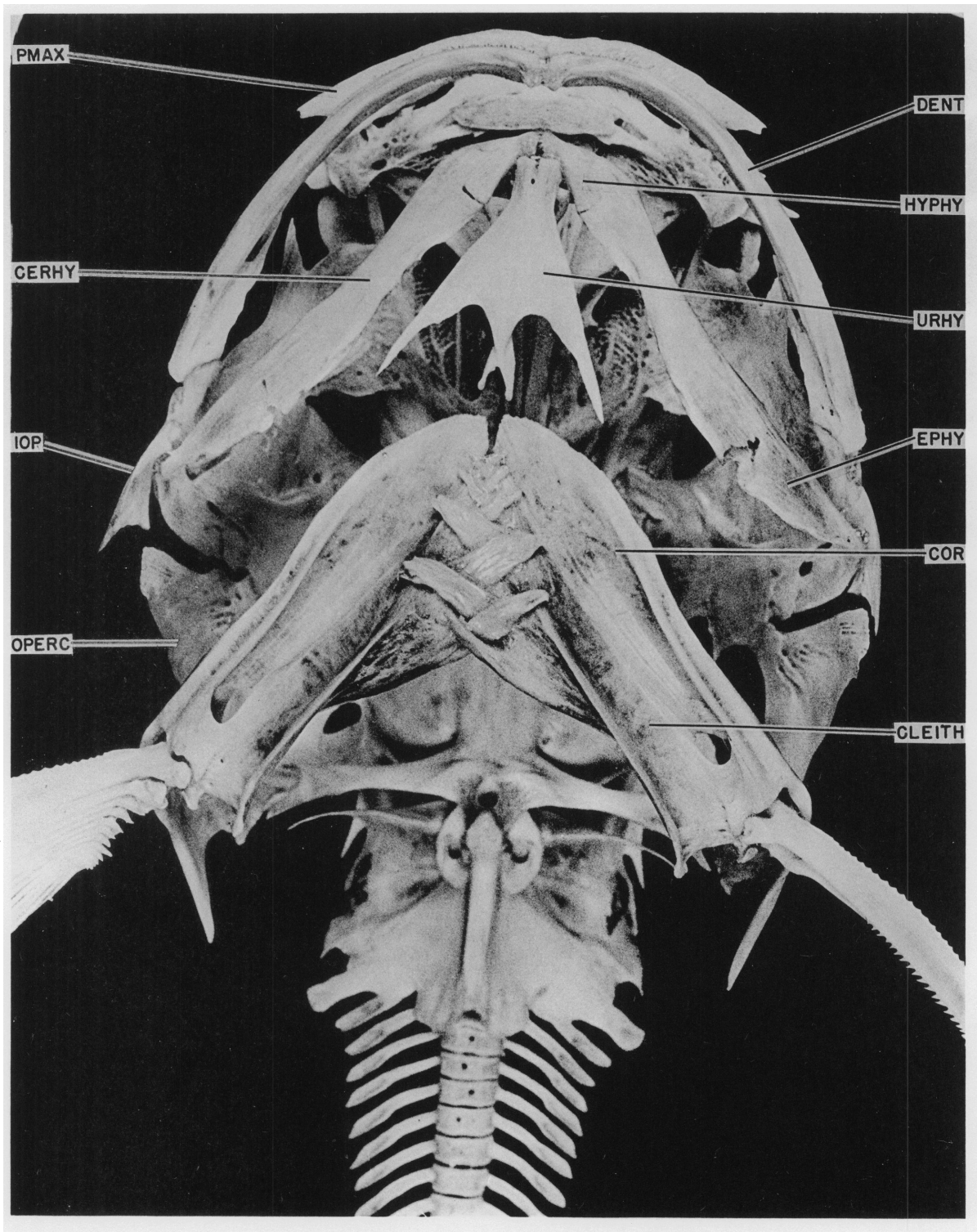
Dorsal view of neurocranium and anterior vertebral complex of *Bagre marinus*. $\times 1$



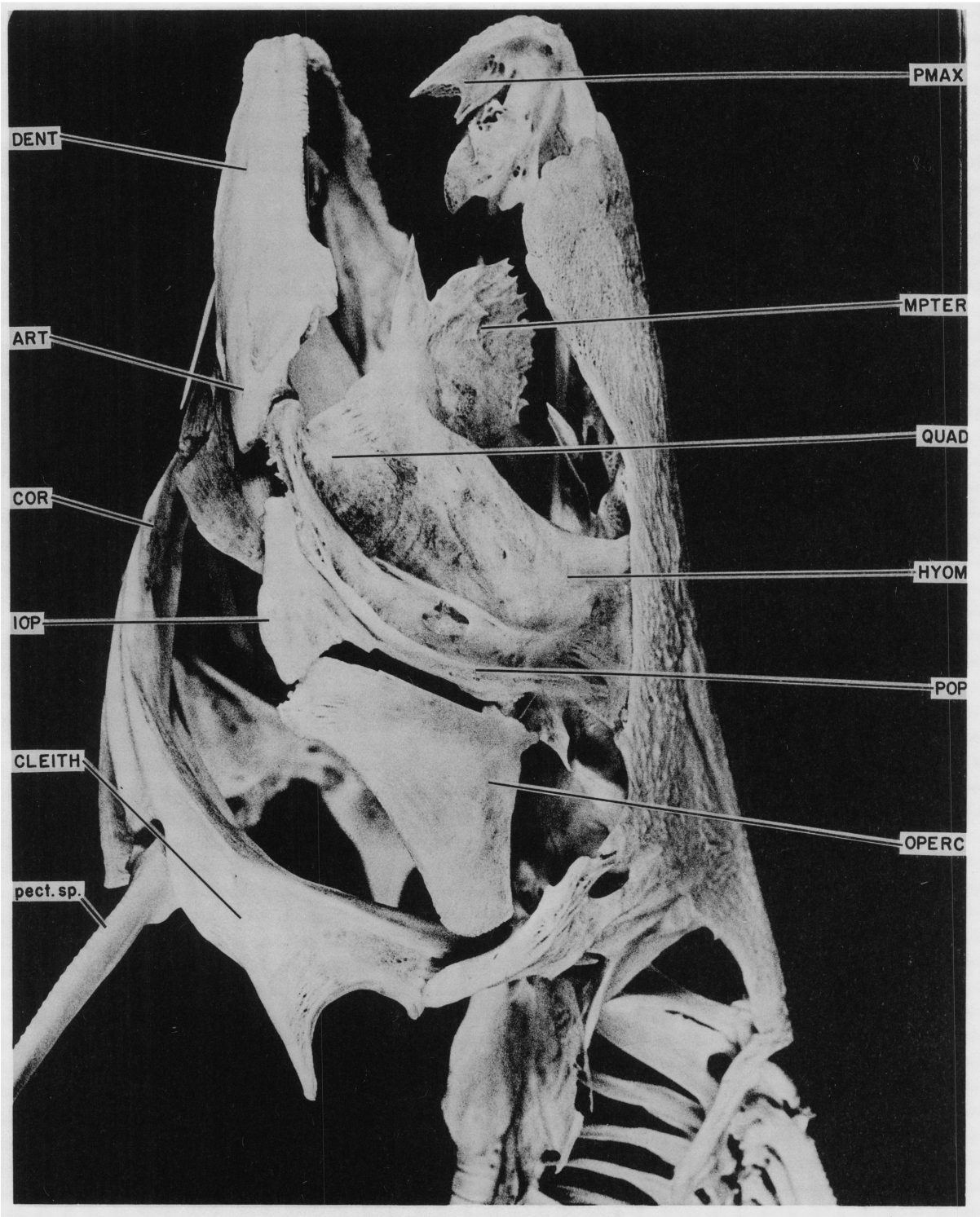
Ventral view of neurocranium and anterior vertebral complex of *Bagre marinus*. $\times 1$



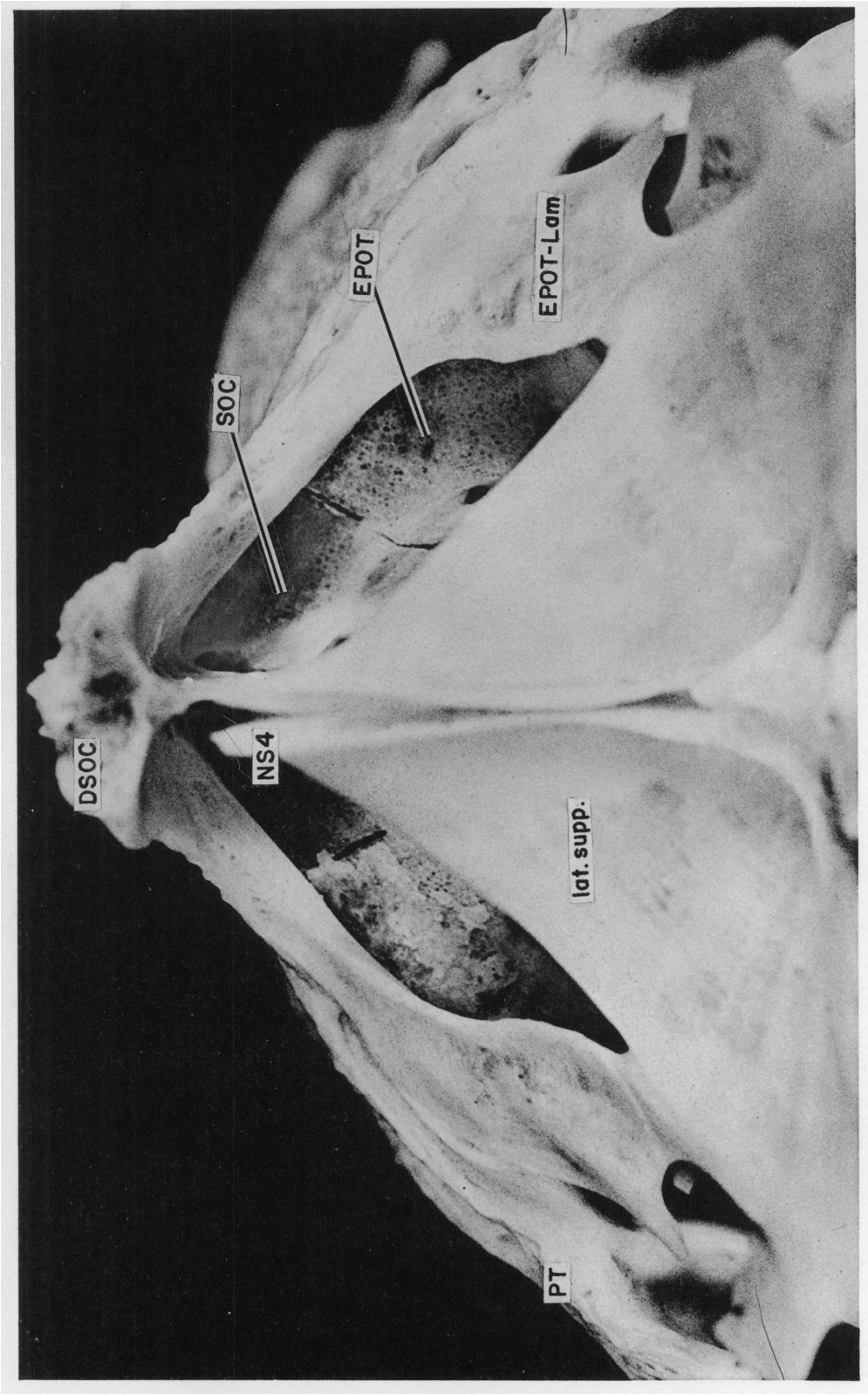
Dorsal view of cranial and pectoral skeleton of *Bagre marinus*. × 1



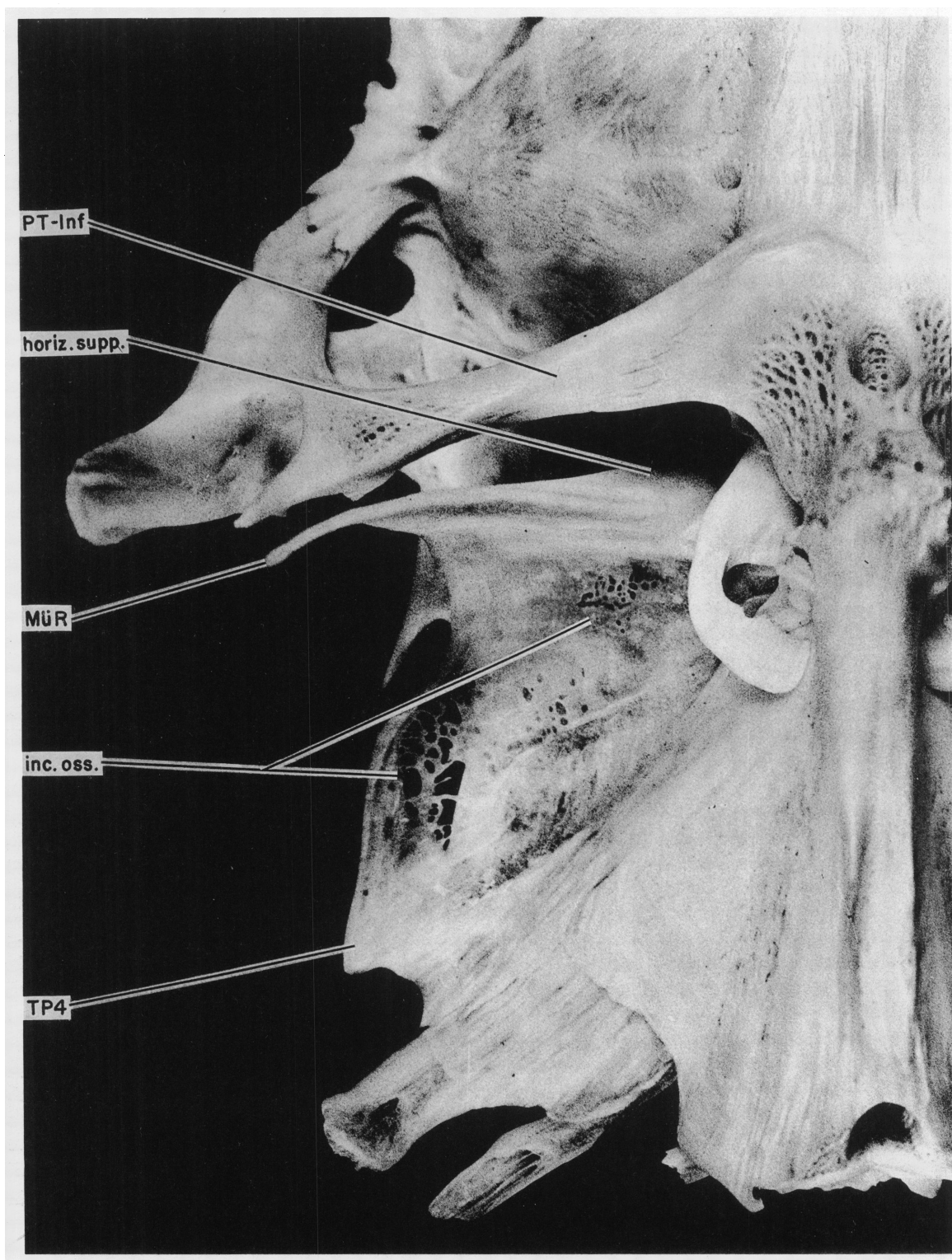
Ventral view of cranial and pectoral skeleton of *Bagre marinus*. × 1



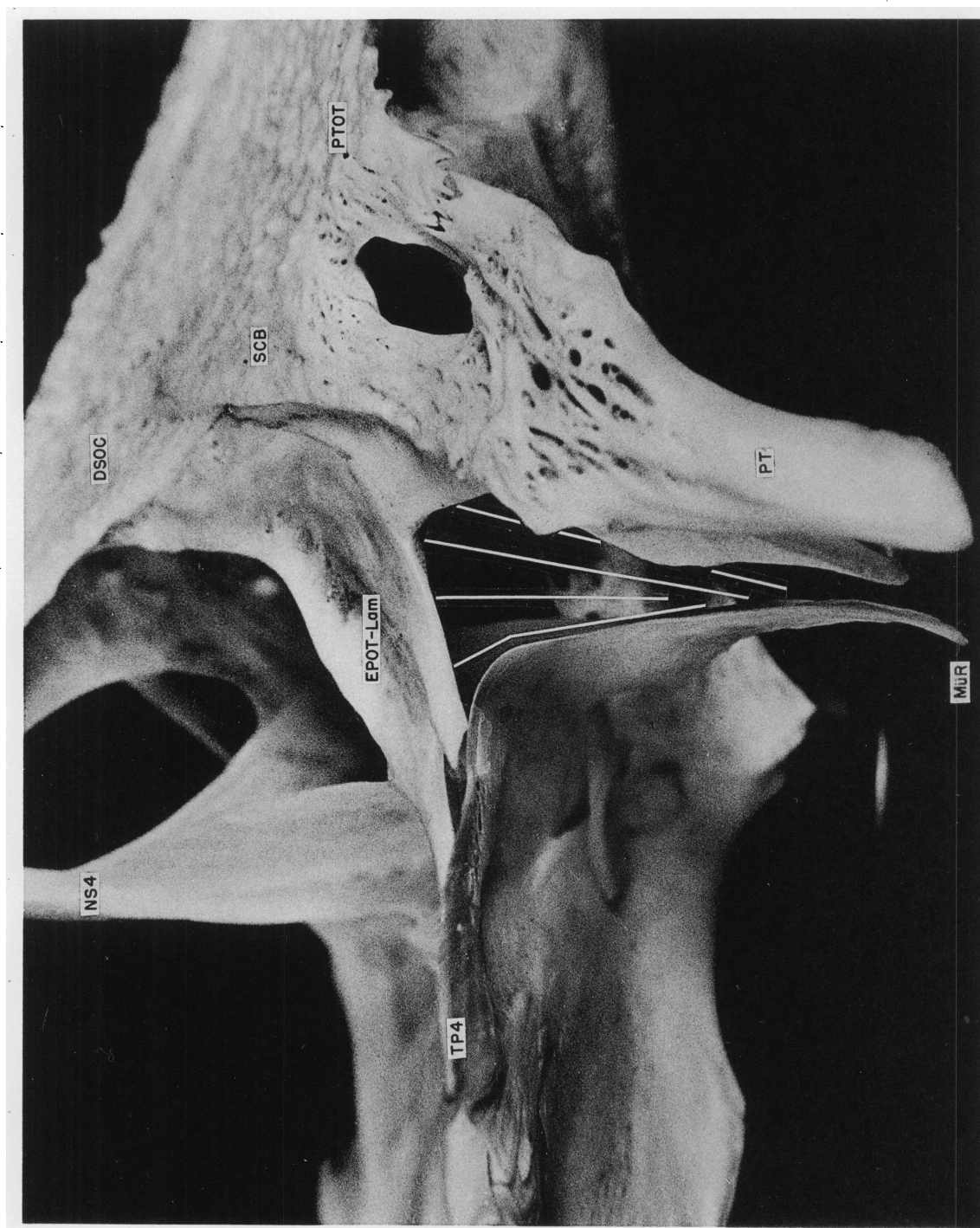
Left lateral view of cranial and pectoral skeleton of *Bagre marinus*. × 1



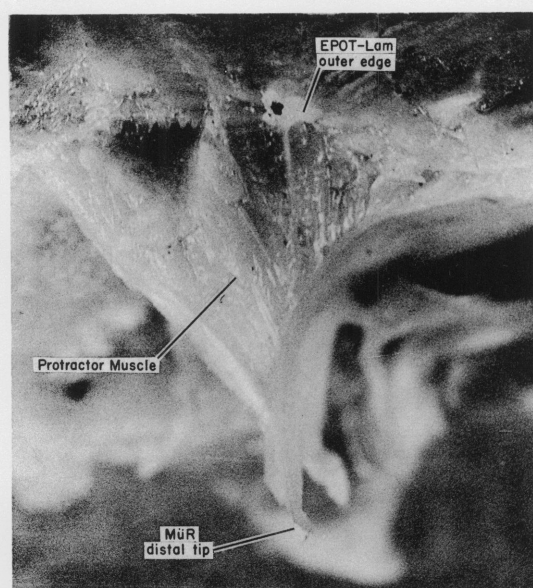
Occipital view of neurocranium and anterior vertebral complex of *Bagre marinus*. X 3



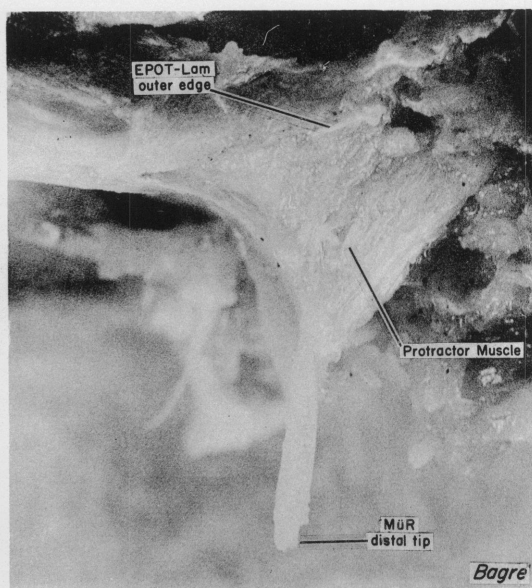
Ventral view of *Springfederapparat* and associated structures of *Bagre marinus*. $\times 3$



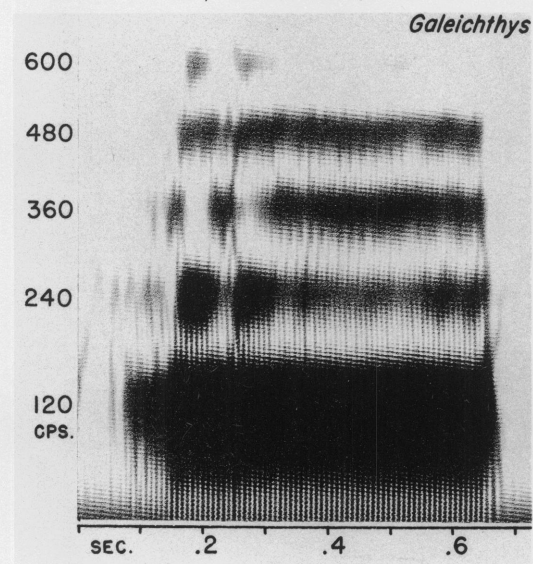
Right lateral view of *Springfederapparatus* and associated structures of *Bage marinus*. White lines represent position of protractor muscle. $\times 5$



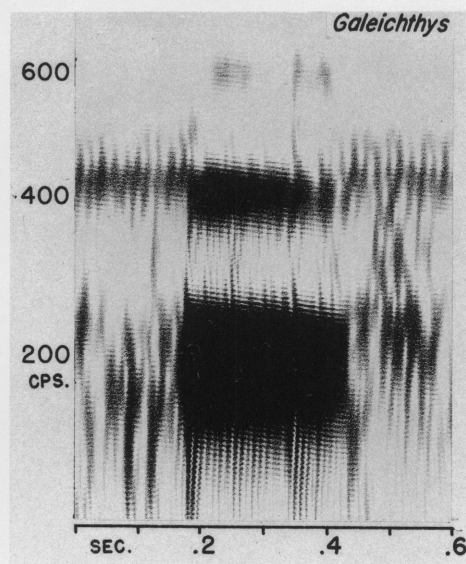
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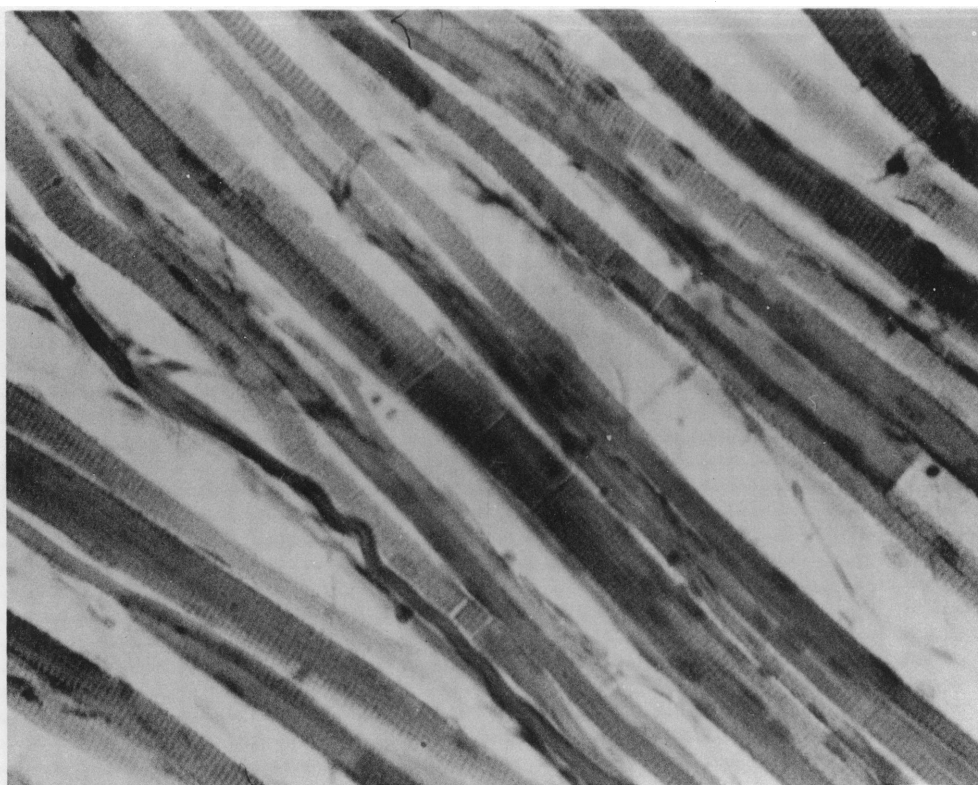
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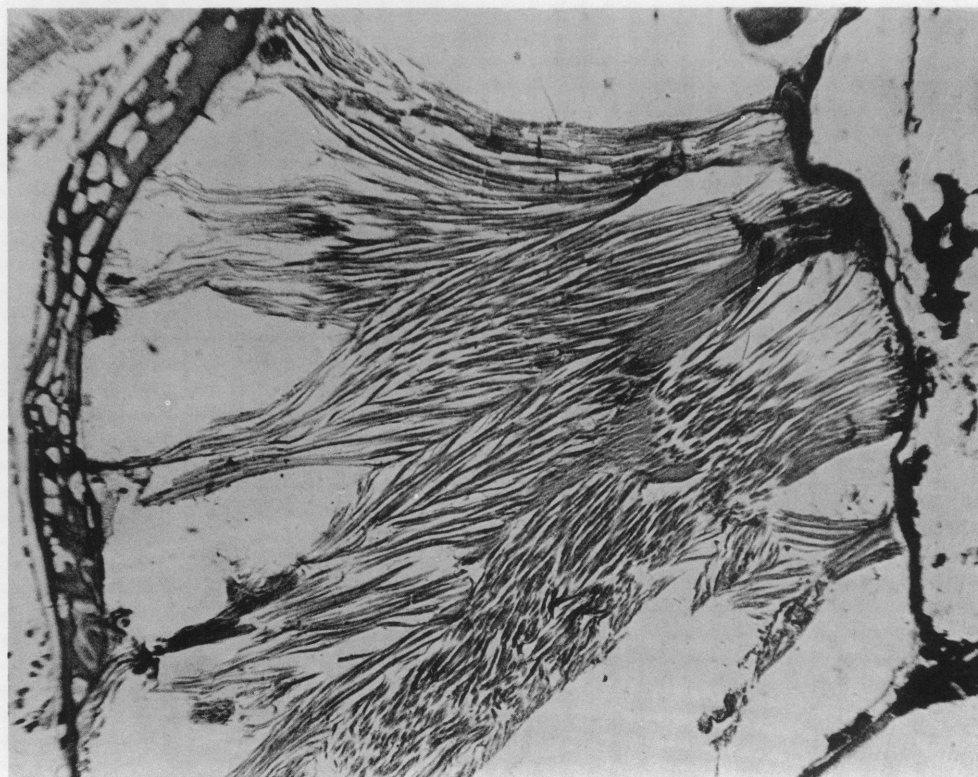
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1, 2. Dissections of preserved specimens to show structure of sound-producing protractor muscle. Post-temporal bone removed; origin of muscle along line indicated as outer edge of epiotic lamina. 1. *Galeichthys felis*, left lateral view. 2. *Bagre marinus*, right lateral view. Both $\times 4$

3, 4. Sonagrams of sounds produced by stimulation of occipital nerve in *Galeichthys*. 3. At 120 pulses per second. 4. At 200 pulses per second

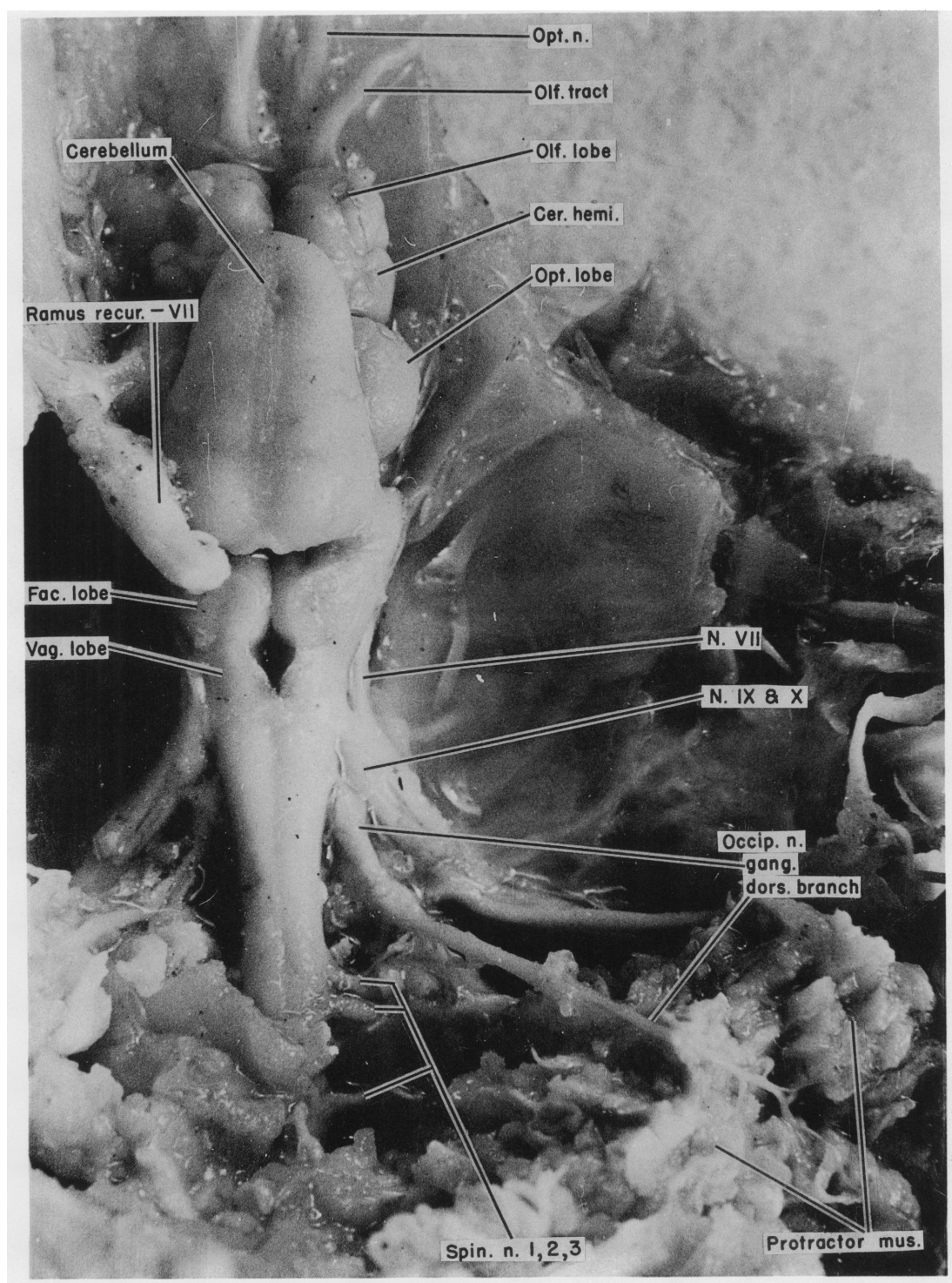


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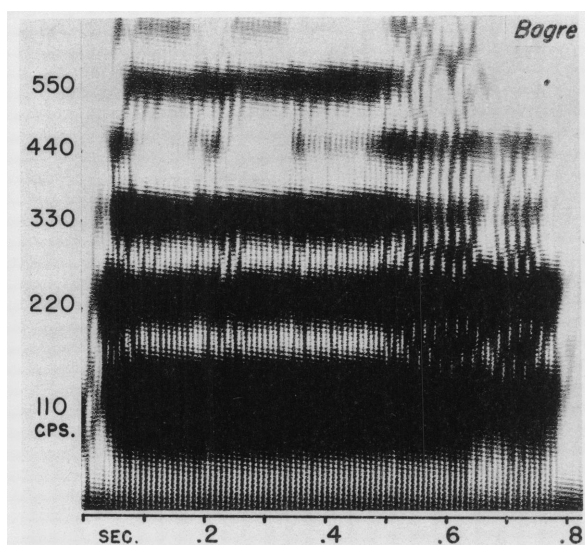
1. Transverse section of juvenile *Galeichthys* in region of protractor muscle. Thick cancellous bone in upper part of picture is a section through epiotic lamina, and dark line where muscle fibers insert is thin shelf formed by expanded fourth transverse process. X 50
2. High-power view of protractor muscle fibers. X 500



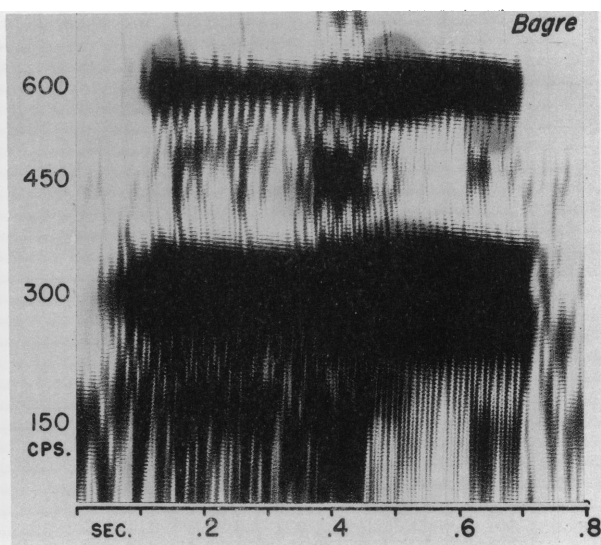
Dissection of brain and cranial nerves of formalin-preserved *Galeichthys felis*. Right epiotic lamina removed to expose dorsal surface of protractor muscle and its innervation by dorsal branch of occipital nerve. Large utricular otolith (lapillus) removed. $\times 3$



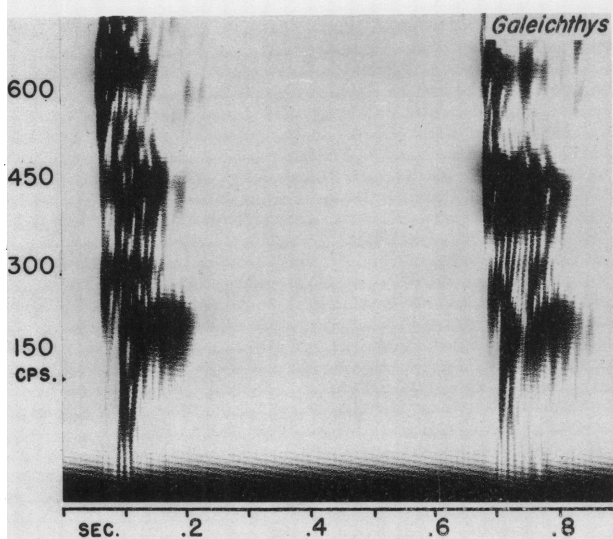
Transverse section of juvenile *Galeichthys felis* at level of occipital nerve, of which dorsal root ganglion and ventral root can be seen on right side of nerve cord. Ventral to nerve cord is portion of perilymphatic cavity (cavum sinus imparis). $\times 75$



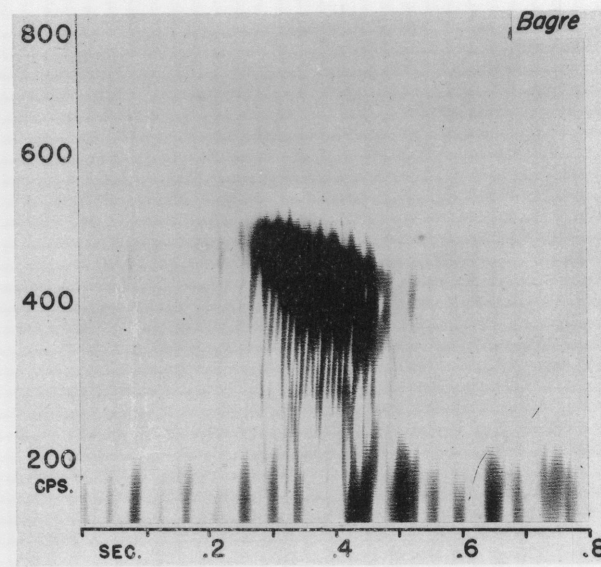
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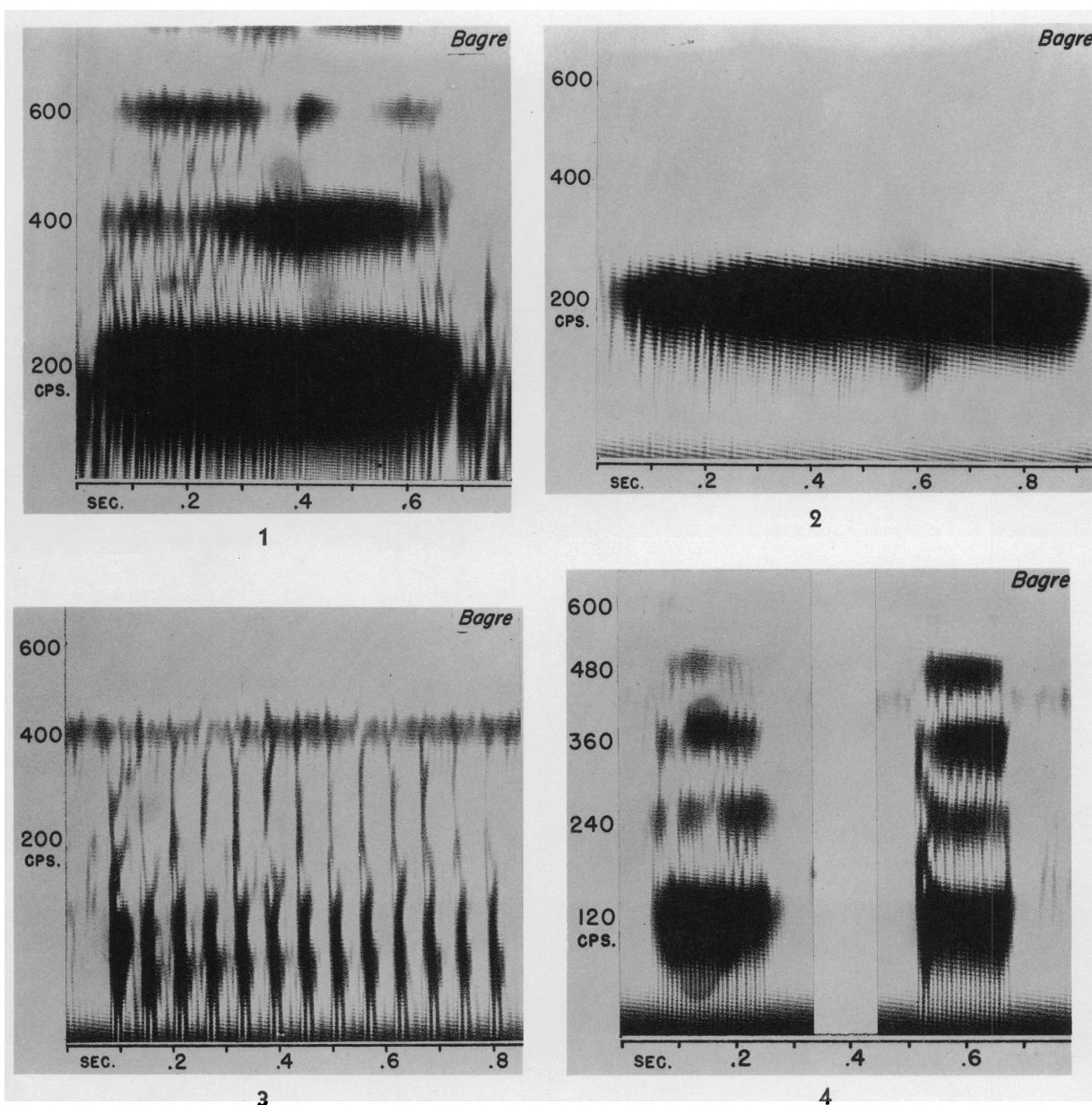


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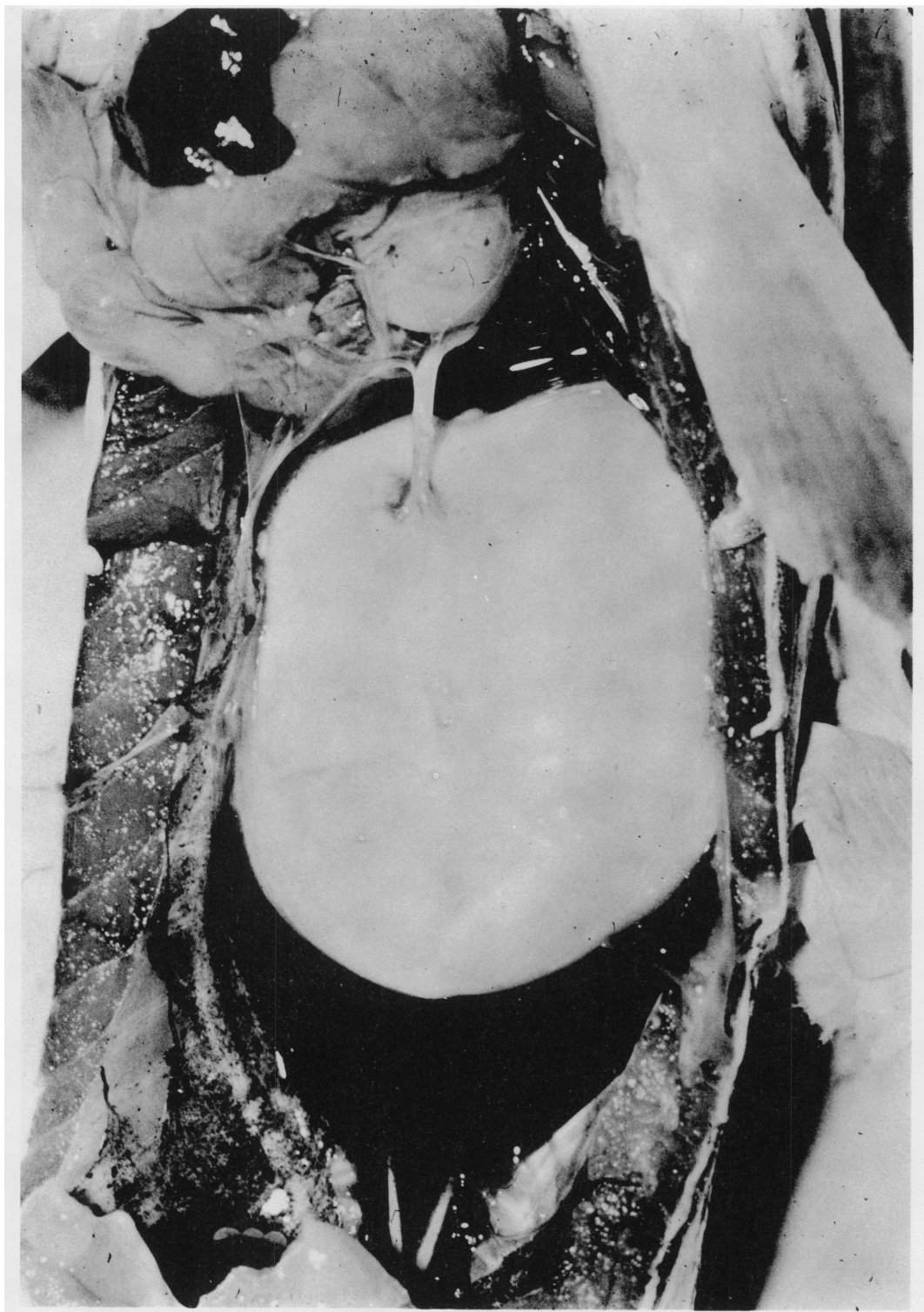


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- 1, 2. Sonagrams of sounds produced by stimulation of occipital nerve in *Bagre*. 1. At 110 pulses per second.
 2. At 300 pulses per second. Note partial response at 150 cycles per second
 3. Sonagram of distress sounds produced by a captive *Galeichthys*
 4. Sonagram of a "sob-like" sound produced by a captive *Bagre*



- 1, 2. Sonograms of sounds produced by stimulation of protractor muscle in *Bagre*. 1. At 200 pulses per second.
2. After entire preparation was covered with fiberglass batting
3. Sonogram of sound produced by stimulation of occipital nerve at approximately 20 pulses per second in *Bagre*. Trace at 400 cycles per second is of external origin
4. Sonogram at left resulted from stimulation of left occipital nerve at 120 pulses per second in *Bagre*. Sonogram at right was produced by same specimen when both occipital nerves were simultaneously stimulated



Dissection showing intact swim bladder of *Galeichthys felis*. Viscera reflected anteriorly, and pneumatic duct is visible. $\times 1$



Dissection of swim bladder of *Galeichthys felis*. Bladder has been split open along frontal plane and its ventral surface reflected anteriorly. $\times 1$

to the anterior ceratobranchials. Although in *Galeichthys* and *Bagre* these muscles appear to be reduced, probably they correspond to the branchial depressors and retractors (pharyngo-clavicularis of McMurrich, 1884, or cleido-branchialis of Fürbringer, 1897). The medial branch continues craniad and innervates a large, conical muscle, the origin of which is the anterodorsal surface of the ventral arm of the cleithrum and the insertion of which is on the posterior surface of the urohyal (see pls. 8, 9, 16, 17 for skeletal parts). This muscle has been variously called "sternohyoid" (Allis, 1897), "hyopectoralis" (McMurrich, 1884), and "coraco-hyoideus" and "cleido-hyoideus" (Fürbringer, 1897). Its function is to draw the floor of the branchial basket ventrad and caudad, expanding the branchial cavity.

The nomenclature and homology of the postvagial nerves in fishes were the subject of a large monograph by Fürbringer (1897). The spino-occipital nerves as a group are characterized by being small and in some instances lacking in dorsal ganglia. The precise distinction between the last spino-occipital and the first true spinal nerve has never been made entirely clear and unambiguous, except on the basis of their emergence from the skull. Fürbringer divided the spino-occipitals into two groups, with reference to their relationships to the segmentation of the occipital region. The nerves immediately behind the vagus he called the "occipital" nerves. These were named "w," "x," "y," and "z," with the posteriormost and most persistent being "z." The occipital nerves emerge through foramina in the exoccipitals, and they were considered as representing the earliest metameres to fuse with the paleocranium to form the neocranium. The second group were called the "occipito-spinal" nerves which emerge through the foramen magnum and out between the occipital ring and the first neural arch. Fürbringer called these "a," "b," and "c" and considered that they represented vestiges of vertebral metameres that secondarily fused with the neocranium. The first true spinal nerve, therefore, was derived from metamere number 4. Teleosts generally lack any vestige of the occipital nerves, e.g., x, y, z, and occipitospinal nerve *a* is also absent. In the Ostariophysi, siluroids included, nerve

c is absent, leaving only the occipitospinal *b*.

Allis (1903) described three occipitospinal nerves in *Scomber*, the first one, presumably Fürbringer's *a*, lacking a dorsal root. In addition, Allis (1897, 1898) disagreed with Fürbringer on the homology and terminology of these nerves. Based upon his work on *Amia*, he stated that the first true spinal nerve actually represented metamere 5 and, in the Ostariophysi, it is nerve *c* that is present, not *b*. Some authors, including Black (1917), have followed Fürbringer's (1897) interpretations. More recently, however, Addens (1933) recommended the use of the term "occipital nerves" for all these structures of uncertain homology between the vagus and the first spinal nerve. The metamerism of the hind part of the skull is subject to a number of different interpretations (Goodrich, 1930), and De Beer (1937) has severely criticized Fürbringer's concepts and reviewed the entire subject of the segmentation of the head.

The possible homology of these occipital nerves with the hypoglossal of higher vertebrates was suggested by Haller (1895) and Fürbringer (1897). Herrick (1899), and several other authors, did not agree with such an interpretation. Most later authors, however, tend to concur with the original theory. Beccari (1922) stated that nerves *z*, *a*, *b*, and *c* combined to form the hypoglossal, and Addens (1933) unequivocally averred that the occipital nerves gave rise to the twelfth.

Wright (1884) described the first spinal nerve (=occipital nerve) in *Ameiurus* as emerging through the exoccipital in two branches. The medial branch turns ventrad and supplies the pharyngo-clavicular (=ceratobranchial retractor) musculature. The lateral branch joins with the first true spinal nerve and supplies some of the pectoral fin muscles. Wright also described a branch innervating the trapezius muscle. Although this was thought to be in error by Herrick (1901), the present report confirms both observations—at least in *Galeichthys* and *Bagre*.

It appears generally true that the spino-occipital nerves are primarily motor and supply some of the hypobranchial musculature. In *Amia* (Allis, 1897) two muscles are innervated: the branchiomandibularis and the sternohyoid. The former is the protractor of the tongue and is not present in teleosts.

The sternohyoid originates from the ventral limb of the cleithrum and inserts on the urohyal. Its action depresses and expands the floor of the branchial cavity. The term "sternohyoid" probably originated with Cuvier, from a superficial resemblance to the sternohyoid in human anatomy. In fishes, obviously there is no sternum as such, and therefore other terms have been used. McMurrich (1884) called it the "hypopectoralis," and Fürbringer (1897) named it the "coracohyoideus" or "cleido-hyoideus." Edgeworth (1911) states that in ontogeny the sternohyoid is derived from the hypobranchial spinal musculature.

In teleosts, the spino-occipital nerves also innervate the pharyngo-clavicularis muscles (Wright, 1884; Fürbringer, 1897). Fürbringer called them "cleido-branchialia." They are present in two pairs (internus and externus) arising from the dorsal surface of the ventral arm of the cleithrum and inserting on the ventral ends of the fifth ceratobranchials. They retract and depress the floor of the branchial

cavity. In *Amia* (Allis, 1897), the same muscles are supplied by a branch of the fifth branchial (vagus) nerve. This fact, plus some ontogenetic observations, led Edgeworth (1911) to conclude that the pharyngo-clavicularis is derived from the fifth branchial myotome.

In most instances, the spino-occipital nerves in teleosts have been found to contribute to the brachial plexus, the anterior portion of which is often referred to as the "ramus cervicalis." In *Ameiurus* (Wright, 1884), there are branches to the abductor and deep adductor of the pectoral fin spine.

The innervation of the protractor muscle of the Müllerian ramus has not been hitherto described, but it seems evident that, in the Ariidae at least, the occipital nerve is the sole supply. From these data it can be inferred that the protractor muscle is most probably derived from the hypobranchial moiety, although its position suggests an origin from epaxial trunk musculature.

PHYSIOLOGICAL ASPECTS OF THE SOUND-PRODUCING MECHANISM

IN BRIEF, the technique consisted of the stimulation of the nerves or muscles with a spike form of repetitive potential. The response of the protractor muscle was an audible sound, the pitch of which corresponded to the frequency of stimulus repetition. The muscle response was detected with a microphone or hydrophone, recorded on magnetic tape, and monitored by earphones and an oscilloscope.

EQUIPMENT AND METHODS

The stimulus source was a variable-frequency, square-wave generator, the output of which was controlled by a telgraph key. By passage through a 500-micromicrofarad capacitor and a pair of silicon diodes, the wave form was changed to a train of spike-form potentials. These were amplified, and the stimulus was applied to the tissues of a decapitated or anesthetized animal by means

of a pair of stainless steel wire electrodes. The electrodes were insulated in plastic and glass except for the terminal millimeter. The output at the electrodes was measured with a vacuum tube voltmeter and monitored visually on an oscilloscope. At frequencies of up to 700 cycles per second, the spike potentials had a rise time of about one microsecond and an exponential decay time of one and eight-tenths to two milliseconds. (See fig. 1.)

The audible response was detected either with a hydrophone, if the preparation was under water, or with a crystal microphone, if in air. The hydrophone was a small barium-titanate crystal unit. In either case, the signal was passed through a voltage pre-amplifier and thence to a magnetic tape recorder. The tape recorder output was monitored with earphones, and the signal was also made visible on an oscilloscope screen.

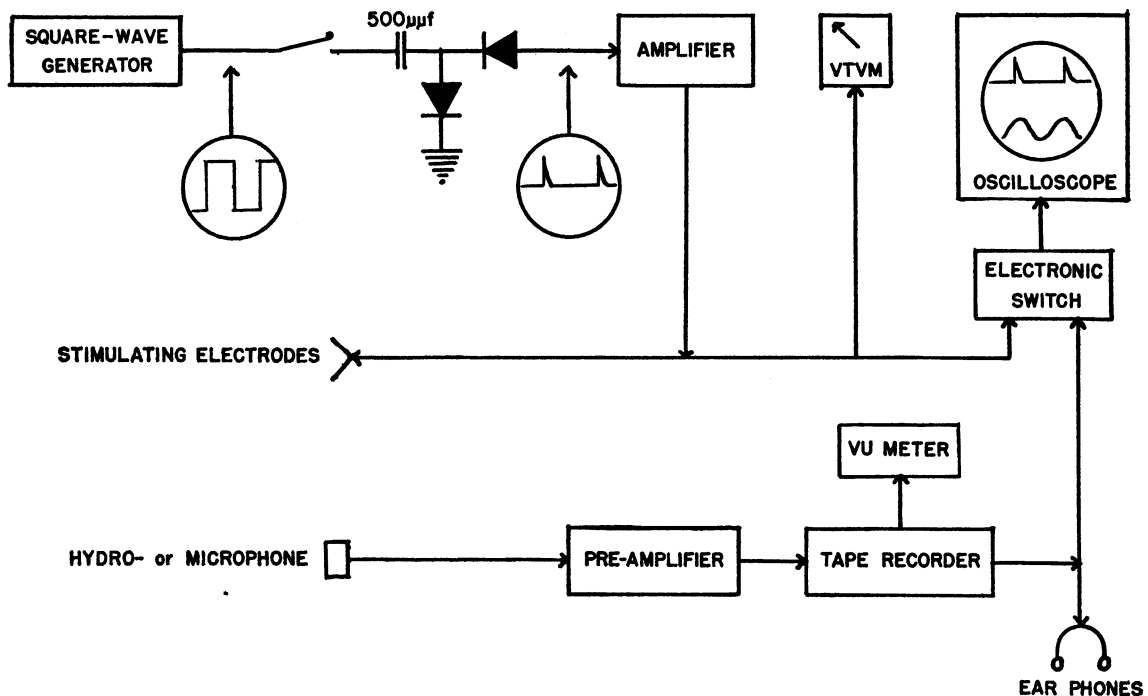


FIG. 1. Block diagram of equipment used in stimulating and recording sound production in nerve-muscle preparations of catfishes.

By means of an electronic switch, both the stimulator output and the response could be observed on the oscilloscope at the same time. The relative response intensity was measured on a VU meter across the output of the tape recorder.

The tape recordings were subsequently analyzed by means of a sound spectrograph (Sona-Graph, manufactured by the Kay Electric Co.). Recording levels and the "re-produce" levels of the Sona-Graph were always monitored with a VU meter to prevent harmonic distortion from overloaded amplifiers. Plates 21, figures 3 and 4, and plates 25 and 26 represent a sample of the records used as data in this section.

The animals used were *Galeichthys felis* and *Bagre marinus* of all sizes from about 4 inches to 15 inches in standard length. The results are based on more than 50 specimens. The fish were immobilized in three ways. One method was to tie them down in a form-fitting basket of stiff wire screening. This was feasible for the smallest specimens. A second method was to cut the head off at a point just anterior to the medulla. The third method was to use a solution of one part in 20,000 of MS-222 in sea water flushed over the gills. The responses to stimulations were the same in all cases.

Stimulation was applied, in some cases, directly to the protractor muscle, by the insertion of the electrodes through the skin at a point just below the lateral edge of the epiotic lamina. Stimulus voltages of 5 volts or more were needed to obtain detectable responses. The voltages given here are as read from a voltmeter calibrated to give root-mean-square values for sine waves, so that the actual peak potentials are somewhat higher. In most cases, the stimulus was applied directly to the dorsal branch of the occipital nerve by the removal of the roof of the skull and dissection along the path of the nerve. Here a stimulus intensity of 0.2 volt was adequate for the obtaining of a clear response from the muscle. The electrodes were about 1 mm. apart and placed directly across the exposed nerve trunk at various points along its length. Except when tetanizing rates and fatigue determinations were desired, the stimulus duration was kept short, i.e., about half a second.

In the majority of the tests, the dissected animal was kept moist with wet paper towels, and a crystal microphone in a thin plastic bag was placed underneath the specimen in the region of its swim bladder. In some cases, the specimen was partially immersed in sea water in a shallow tray, and the hydrophone was placed a few inches away. In a few tests, stimulating electrodes were inserted into both protractor muscles, and the anesthetized animal was immersed in a 15-gallon aquarium, with a hydrophone several inches away, i.e., in an effort to duplicate conditions under which some spontaneous sounds were recorded.

SONIC PROPERTIES OF PROTRACTOR MUSCLE

The establishment of the protractor muscle as the sound producer and the occipital nerve as its innervation was accomplished by a trial-and-error method. Various nerves and muscles were stimulated with a spike-potential train of 100 pulses per second. At first, a stimulus of about 10 volts was used across the entire pectoral region of an unanesthetized animal. This evoked an audible response of 100 cycles per second. Gradually, with the use of lower voltages and more localized stimuli, the exact source of the sonic response was determined. This was the protractor muscle (described above), and its response could not only be heard but felt. In an anesthetized specimen with its viscera and swim bladder removed, the vibration in response to electrical stimulation could be felt by placing the fingers against the inner surfaces of the *Springfederapparat*. This observation was also reported by Sørensen (1894) by which he demonstrated the sonic function of the "elastic spring" in *Doras*. In his experiment the fish was not anesthetized and was producing sounds spontaneously. I was able to duplicate Sørensen's observations in both *Galeichthys* and *Bagre*. Cutting the fibers of the protractor muscle resulted in a complete loss of audible response, whereas considerable damage can be done to neighboring pectoral musculature without destroying sound production. Damage to the epiotic lamina or Müllerian ramus also destroyed sound production.

Similarly, the application of a stimulus of

100 pulses per second to various parts of the nervous system showed that the dorsal branch of the occipital nerve was the sole motor innervation of the protractor muscle. A spectrogram of a sound produced by a stimulus of 120 pulses per second is shown in figure 3 of plate 21.

The fact that the protractor muscle and its nerve could respond to a stimulus of 100 pulses per second with a sound of 100 cycles per second without immediately going into tetany was itself considered remarkable. All other muscles that could be tested became tetanized immediately, and, indeed, they became tetanic at stimulus frequencies of more than 10 pulses per second. It was of interest, therefore, to determine the limits of frequency response of the protractor muscle before it became tetanized. In all these tests, the occipital nerve was stimulated near its base at the medulla with the minimum voltage (0.2 to 0.4 volt) necessary to evoke a readily detectable and measurable response. Lower voltages or greater distances between electrodes produced proportionately lower intensity responses. Such a decremental response was undoubtedly the result of the stimulation of part of the nerve fibers. Above a given stimulus voltage, there was no increase in response intensity, which indicated that a maximum of nerve fibers were firing. Stimulus tests were spaced about one minute apart, and after each higher-frequency stimulus a stimulus of 100 pulses per second was used as the next test. In this manner the nerve-muscle preparation was given a period of rest, and a constant check on possible effects of fatigue on response intensity could be kept.

FREQUENCY RESPONSE: The graphs (fig. 2) summarize the data on frequency response in both species. Each point represents an average of five or 10 observations. A total of 15 animals (10 *Galeichthys* and five *Bagre*) of mature size were used. In some individuals, a complete curve was obtained in a single series of stimulations, but in most cases relative values of only two or three frequencies were possible and reliable. Relative intensity measurements were extremely variable, because the slightest change in the position of the animal, electrodes, or microphone between tests altered the VU-meter reading

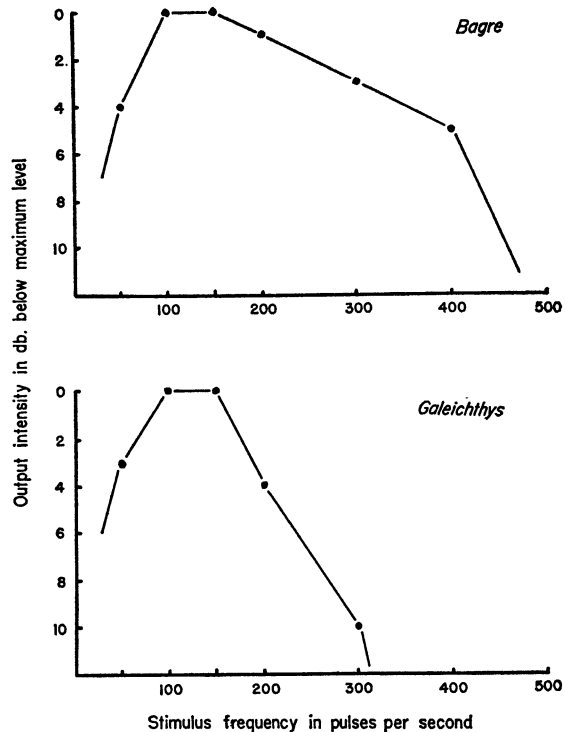


FIG. 2. Graphs showing differences in frequency response of the sonic apparatus in *Bagre* and *Galeichthys*, as determined from artificial stimulation experiments.

drastically. Thus a large number of determinations were dismissed as unreliable, and only those that could be repeated several times in a single preparation are included here.

Despite the few data, the results are quite indicative. In both species, the best response was to a stimulus of from 100 to 150 pulses per second. The response intensity dropped sharply at 50 pulses per second. At stimulus frequencies of over 150, there was a clear difference between the two species. In *Galeichthys*, there was a 4-decibel drop at 200 pulses per second. At 300 pulses per second, the response intensity was approximated at about 10 decibels below that at 150, and the muscle became tetanized in less than two-tenths of a second. At 400 pulses per second, the tetanization was immediate, and there was no sonic response. Figures 3 and 4 of plate 21 show sound spectrograms resulting from stimulations at 120 and 200 pulses per second.

TABLE 1
TIME (IN SECONDS) IN WHICH PROTRACTOR
MUSCLES REACHED TETANY

Stimulus Frequency in Pulses per Second	<i>Galeichthys</i> (Average of 10)	<i>Bagre</i> (Average of 5)
20	15	20
50	12	18
100	3	12
150	3	12
200	0.3	3
300	<0.2	1.5
400	Immediate	0.4
500	Immediate	<0.1

In *Bagre*, there was only a 1-decibel drop at 200 pulses per second, a 3-decibel drop at 300 pulses per second, and a 5-decibel drop at 400 pulses per second. At 500 pulses per second, tetanization occurred in less than one-tenth of a second, and the response intensity could not be measured, but a brief sound was detectable at a pitch of 500 cycles per second. Sound spectograms (pl. 25, figs. 1, 2) show responses to stimulations of 110 and 300 pulses per second.

In short, the sound-producing system in *Bagre* was capable of a frequency response almost an octave higher than that of *Galeichthys*.

TETANIZATION: The rate at which the protractor muscle became tetanized at various frequencies is obviously a factor in the responsiveness of the system. In this respect also there was a difference between the species. Table 1 shows the tetanizing times at various frequencies. These were measured as the length of time from initiation of the stimulus to a point at which the sonic response could no longer be detected. The time was determined by the measuring of the magnetic tape on which the sound was recorded.

In order to test the effects of fatigue after a tetanizing stimulus, the preparation was given a 30-second rest period and then stimulated for half of a second at 100 pulses per second. In all cases, the response was at least 4 decibels lower than at a previous stimulus of 100 pulses per second. Following a two-minute rest, tetanization took place more

rapidly, but after a half-hour rest, the original determinations could be replicated. Probably the abnormally strong and prolonged stimulation produced fatigue in the muscle, and possibly accumulation of the by-products of fatigue reduced the resistance of the muscle to tetanization.

The physiology of a muscle capable of a response to such high rates of stimulus repetition is of interest. Fast-acting muscles of such a nature are not common but are widely distributed among animals. The best known are the flight muscles of insects (Gilmour, 1953; Chadwick, 1953). Some species exhibit a contraction and relaxation rate of up to 1000 per second, but 200 to 300 is the more common range. It is not known, however, if such muscles are actually capable of responding *in toto* to a stimulus administered with such a frequency. Among vertebrates, the muscle with the highest known fusion frequency is the internal rectus of the cat, in which complete tetanization is achieved at a stimulus repeated at 350 pulses per second (Cooper and Eccles, 1930). The swim-bladder muscle of the toadfish (*Opsanus*) is a fast-acting tissue comparable to the protractor muscle in the catfishes. Skoglund (1959) showed that it had a contraction-relaxation cycle of 10 to 15 milliseconds, and Fawcett and Revel (1961) studied it with techniques of the electron microscope. Their study revealed a highly developed sarcoplasmic reticulum which is presumed to be an important factor in the conduction of the impulse from the motor end plate to the contractile elements within the muscle fiber. Cytological investigations of this type on the catfish protractor muscle would seem to be highly desirable, with a view toward an investigation of both its fast-acting and quick-recovery properties.

CHARACTER OF NORMAL AND ARTIFICIALLY PRODUCED SOUNDS

Spontaneously produced sounds in marine catfish have been variously described as "grunts," "pops," and so on by Dobrin (1947), Knudson, Alford, and Emling (1948), and Kellogg (1955). Tavalga (1960) used spectrographic analysis on these sounds, and the following description is based mainly on that report.

GALEICHTHYS FELIS: Sounds of animals both under captive conditions and in the

field are all similar in possessing a fundamental frequency at about 150 cycles per second and several harmonics at intervals of 150 cycles per second (pl. 25, fig. 3). The durations vary from 20 to 40 milliseconds, with distress sounds tending to be longer (over 100 milliseconds) than those uttered during the formation of nocturnal schools. The harmonics were found to be variable in strength and number, and under some conditions the fundamental of 150 cycles per second could not even be detected, although the spacing of the harmonics indicated that it must be present.

BAGRE MARINUS: Distress sounds from these animals were essentially the same as those of *Galeichthys*, with a fundamental at 150 cycles per second. Sounds during night schooling were, however, quite different. These were long, sob-like cries, with a distinct fundamental at about 400 cycles per second, and a duration of almost two-tenths of a second (pl. 25, fig. 4).

Although the nocturnal schooling sounds could not be elicited at the experimenter's will, the distress sounds of both species were easily evoked by prodding or electric shock (D.C.). Thus the harmonic content of these sounds could be analyzed under various conditions. It was found that the surrounding environment and the distance of the microphone or hydrophone made a considerable difference in the strength and occurrence of harmonics in these distress sounds.

In a small, 2-gallon aquarium, with the hydrophone within an inch of the animal, the sounds were almost pure tones at a frequency of 150 cycles per second. Using large wooden tanks 6 feet or more in the longest dimension resulted in an almost complete loss of the fundamental and an emphasized harmonic at 300 cycles per second. If the animal was held in the air, with it and a microphone wrapped in acoustical padding (fiberglass batting), the sound output was a pure tone at 150 cycles per second. Actually, the harmonic content of the catfish grunts could be altered easily by changing the conditions under which the recording was made. If a sound speed in sea water of about 5000 feet per second is assumed, the wave length at 150 cycles per second would be about 33.3 feet; and at 300 cycles per second, about 16.6 feet. Thus a large aquarium could function as a

half-wave resonating chamber. Standing waves created under these and similar circumstances could conceivably reinforce or dampen certain frequencies and even create harmonics that did not exist in the original sound source. Recording under water always presents such problems more acutely than that in air, because it is virtually impossible to do away with the ever-present, reflecting, air-water interface. As much as 99.9 per cent of sound propagated in water is reflected back from the surface layer (Vigoureux, 1960; Horton, 1959). It can be concluded that, unless sound reflections are rigidly controlled or eliminated, only the fundamental frequency of these fish sounds is of any significance with regard to interpretations of mechanisms of sound production.

The artificially produced sounds, by stimulations of the occipital nerves, were with few exceptions at a pitch that exactly matched the frequency of the stimulus repetition rate. The few exceptions occurred sporadically with specimens of *Bagre*. In some cases a stimulus of 400 pulses per second produced a fleeting response at a fundamental pitch of 200 cycles per second, and in one instance a stimulus of 300 pulses per second produced a response of 150 cycles per second (pl. 25, fig. 2). In each case the stimulus level was a low one, and unfortunately the situation could not be duplicated except by chance. Very probably the nerve was responding to alternate pulses.

Spectrographic analysis of the responses to pulsed stimuli showed the presence of harmonics. However, the occurrence and strengths of the harmonics were extremely variable, and, as with the spontaneous sounds, the harmonic content could be varied with the environmental conditions. Stimulation at 150 pulses per second in a large aquarium would almost duplicate the harmonic content of spontaneous sounds uttered in the same container. Plate 26 shows sound spectrograms of an artificially stimulated (200 pulses per second) specimen before (fig. 1) and after (fig. 2) the preparation was covered with fiberglass batting. Furthermore, stimulations at 20 pulses per second or less produced completely non-harmonic sounds (pl. 26, fig. 3). This is, then, a second indication that harmonics are not intrinsic in the sonic mechanism.

In most of the tests, only a single occipital nerve was stimulated. In a few cases, a bilateral stimulation was accomplished. Two pairs of electrodes were connected in parallel, one pair across each of the occipital nerves. The distances between the electrodes, their position across the nerves, and the stimulus levels were all adjusted so that the response from each side alone was measured, and both were equivalent. When both nerves were thus stimulated at 100, 150, and 200 pulses per second, the response intensity was increased by about 1 decibel over that of a unilateral response. Harmonically there was no significant difference between a unilaterally and a bilaterally stimulated response (pl. 26, fig. 4).

EFFECTS OF SWIM-BLADDER DAMAGE ON SOUND OUTPUT

The anatomy of the swim bladder in *Arius* and many other siluroids has been described in detail by Bridge and Haddon (1893). The following is summarized from descriptions by Tavalga (1960) for *Galeichthys felis* and *Bagre marinus* (pls. 27, 28).

The swim bladder is composed of a soft, fibrous, slightly elastic tissue. It is ovoid in shape, with a straight, flattened, anterior margin, and comes to a rounded apex posteriorly. A thin pneumatic duct connects the ventral surface to the anterodorsal wall of the cardiac stomach (pl. 27). The bladder is never strongly distended, and puncture of the wall causes little or no visible collapse. There are no muscles inside, outside, or connected to the bladder. No red glands are present. Internally there are a large anterior chamber and a smaller posterior chamber (pl. 28). The latter is divided by a sagittal septum and two secondary transverse septa. All chambers are connected by dorsolateral passageways through the transverse septa. The internal architecture is strongly reminiscent of a series of sound-absorbing and directing baffles within a loud-speaker enclosure, particularly in *Bagre*, in which the walls of the posterior chamber possess numerous small pockets and other irregularities. The posterior chamber is attached loosely to the dorsal body wall, but the anterior chamber is firmly knitted dorsally to the thin shelf of bone formed by the fourth and fifth pairs of parapophyses, including the entire inner surface of the

Springfederapparat. A pair of tough, flat tendons extend along the anterior margin of the bladder from the distal tips of the Müllerian rami to the protruding subvertebral process.

In most cases, an unanesthetized animal ceased sound production when immobilized and dissected. A single specimen of *Galeichthys*, however, continued a steady stream of grunts, even after complete evisceration and destruction of its swim bladder. The sounds were recorded but not measured at that time, but the relative intensities and harmonic contents were analyzed from the tape recordings. Evisceration had no effect on the intensity or quality of the sounds, nor did a small incision into the ventral surface of the swim bladder. As the swim bladder was opened up, the sound output became greatly reduced, to a level at least 10 to 15 decibels below the original. Although the recording was made in air, with a crystal microphone and considerable background noise, weak harmonics at 300 and 400 cycles per second were still detectable even after complete excision of the swim bladder except for the portion attached to the *Springfederapparat*.

The same observations were duplicated with anesthetized, artificially stimulated specimens. In air, the destruction of the swim bladder reduced the sound output at the frequencies tested (100 and 150 pulses per second) by at least 10 decibels, but did not effect the quality of the sound. Similarly, under water, if the swim bladder were ruptured and permitted to fill with water, the sound output dropped at least 20 decibels, almost to inaudibility. Filling the swim bladder with water, while the specimen was in air, gave essentially the same results. With the attachment of a large hypodermic syringe to the pneumatic duct, the air pressure in the swim bladder could be changed. An increase of the pressure almost to the bursting point had no detectable effect on either the intensity or the quality of the artificially produced sounds. A reduction of pressure gradually reduced the sound output, but again the quality of the sound remained unaffected.

From the above it can be concluded that the air bladder serves as a means of transmitting and amplifying the sound produced at the *Springfederapparat*.

MECHANICS OF SOUND-PRODUCTION: CONCLUSIONS

IT HAS ALWAYS BEEN ASSUMED that the structure of the sonic organs determined the timbre and pitch of the sound emitted. The acoustical characteristics of the swim bladder were considered as fixing the character of the sounds. In the marine catfishes at least, the evidence points strongly to the fact that the fundamental frequency of the sounds is the direct equivalent of the frequency of contraction of the protractor muscles. The stiff, spring-like, Müllerian ramus acts as the antagonist of the muscle. The ability of the protractor muscle to contract at such frequencies, i.e., its remarkably rapid contraction-recovery cycle, resides in four factors.

First is its high vascularization, as evidenced by its color and spongy consistency. A rich blood supply and drainage would be essential. The relatively small diameter of the muscle fibers increases surface area and enhances the efficiency of exchange of materials between the blood and the tissue.

Second is the intrinsic cellular structure and physiology of the protractor muscle fibers. The small size of the fibers, the closely packed myofibrils, and small amount of sarcoplasm are only indicative of fast-acting properties. It will be necessary to do some fine cytological and histochemical work to establish further the relation between cytology and cytophysiology. In addition, it would be of interest to know what the contractile properties of isolated fibers and fiber bundles would be when removed from the restretching effect of the stiff Müllerian ramus.

A third factor is the ability of the occipital nerve fibers to fire with such a rapid recovery rate. This is under the control of some unknown central medullary mechanism with the unique ability to trigger and regulate the train of stimuli. Here is a most intriguing problem for the neurophysiologist. Even if it be assumed that in natural sound production all fibers do not fire simultaneously, there still must be an unusually rapid recovery rate in this neural mechanism.

Fourth is the structure of the Müllerian ramus. Its very stiffness is a considerable advantage, because it produces a quick return with the minimum of overshoot. It might be

postulated that the spring has a natural oscillating frequency of its own and that the muscle simply "twangs" it. If this were so, then the pitch of the natural sounds would be quite high, at least over 1000 cycles per second, because the spring is short and extremely stiff. In acoustical and electronic terms, the system has a low compliance and a high damping factor. Although this property usually indicates a poor low-frequency response, it does increase the speed with which the muscle fibers are returned to "rest" position. Furthermore, the system would tend to be extremely resistant to the effects of reverberations and, as a result, to the production of harmonics.

Possibly the differences in sonic properties between *Bagre* and *Galeichthys* are the result of differences in the compliance of the Müllerian ramus. The extent to which the ramus is bent during the contraction phase of the muscle is not known, except that it is a very small, grossly imperceptible distance. The distal tip of the Müllerian ramus in a freshly dissected specimen or a dried skeleton can be moved dorsally only. In *Galeichthys*, it takes a weight of 10 to 20 grams to deflect the tip a distance of 0.5 mm. Larger specimens have stiffer, less compliant springs. In *Bagre*, the limit of deflection is only 0.25 mm., and a force of 50 grams is necessary to accomplish this. The structure of the supporting bones also indicates that *Bagre* has the system of lower compliance. This factor may account for the higher limits of frequency response in *Bagre*.

The role of the swim bladder in sound production appears to be relatively minor. The evidence indicates that the timbre, i.e., harmonic content, of the sounds is not a function of the bladder, but is extrinsic. It is clear, however, that destruction, severe damage, or removal of air from the swim bladder causes a large decrease in the amplitude of sounds produced by the *Springfederapparat*. In effect, then, the bladder amplifies the sound, but I can suggest no mechanism by which amplification in the true sense can be achieved, if by amplification we mean the increase in amplitude, i.e., amount of sound

energy. Vigoureux (1960) pointed out that water has an extremely high impedance, i.e., resistance to initial propagation, as compared to air. Energy transmission, on the other hand, is more efficient in water than in air. The problems of under-water sound production and the physics of water-borne sound are reviewed by Horton (1959) and Richardson (1957). Comparatively, the area of the vibrating *Springfederapparat* is much smaller than that of the entire swim-bladder wall. If we assume that the function of the air within the bladder is simply to transmit and distribute the sound energy from the *Springfederapparat* to the bladder wall, then the bladder acts as an impedance matching device and not as an amplifier. An analogy can be made here with function of the paper cone of a loud-speaker which transmits the vibrations of the voice coil to the air. We can probably ignore the rest of the fish, because, in the words of Griffin (1955), it is essentially transparent to water-borne sound. This contention has been made by many other authors, including Marshall (1951). Jones and Pearce (1958) showed that with a 30-kilocycle sonar signal about 50 per cent of the sound energy of the echo was caused by the swim bladder.

What, then, remains as the function of the swim bladder in these catfishes? Its vascular supply is small, and it lacks red glands, so that its role in gas secretion and storage is probably negligible. Very likely its structure is important in sound reception, as is evidenced by the insertion of the tripus into its dorsal wall. The sensitivity of these ostario-

physine fishes to frequencies of more than 1000 cycles per second could well be enhanced by the swim bladder which could act as an acoustical discontinuity and, again, as an impedance matching device. The elaborate septa and irregularities in the inner wall might have two functions. One would be to prevent the internal echoes that would be possible at higher frequencies. In air, a half wave length at 2000 cycles per second would be in the order of 3 inches, a magnitude within the dimensions of the average catfish swim bladder. Among the catfishes, *Ameiurus* has been shown to have an extremely high auditory acuity dependent on its swim bladder (Kleerekoper and Roggenkamp, 1959). Another function might be suggested, that of sound localization. Conceivably a sound-receiving device with transverse baffles as present in the catfish swim bladder would tend to have an axis of optimum response. Indications are that at least one ostariophysine fish (*Semotilus*) possesses localization abilities (Kleerekoper and Chagnon, 1954). To carry this hypothesis one step farther, is it possible for the entire sound-producing and receiving complex to act as an echo-ranging mechanism? Considering the absence of any direct evidence for such an hypothesis, I advance it here simply as an intriguing speculation. Griffin (1955) suggested the possibility of an echo-ranging method in fishes based on the detection of modal intensity changes in standing waves, in which case the emission of sounds without intrinsic harmonics would be advantageous.

SUMMARY

THE SKELETAL BASIS of the sound producing mechanism in the ariid catfishes *Galeichthys felis* and *Bagre marinus* consists of a thin shelf of bone which is firmly attached to the anterior dorsal wall of the swim bladder. This so-called "elastic spring," or "*Springfederapparat*," is formed from the parapophysis of the fourth vertebra. The anterior ramus of this parapophysis, herein named the "Müllerian ramus" (after Johannes Müller who, in 1842, first described the structure), is the main vibrating element in sound production.

The skulls and anterior vertebral complexes of *Galeichthys* and *Bagre* are figured and described, with comparisons with a non-sonic silurid form, *Wallago*.

The "protractor muscle" (so named by Bridge and Haddon in 1893) which activates the Müllerian ramus is a highly vascularized conical muscle, the origin of which is on the under side of the epiotic lamina and insertion on the Müllerian ramus. It is innervated by the dorsal branch of the occipital nerve. The relationship of this nerve to the cranial nerves of higher vertebrates is controversial, but it is probably homologous with the hypoglossal (XII).

Stimulation of the protractor muscle or its nerve supply with repetitive spike-form potentials results in an audible sound output from the *Springfederapparat*. This response can be recorded and analyzed, and its funda-

mental pitch is equivalent to the pulse frequency of the stimulus. The protractor muscle is remarkable in that it can withstand stimulations of 300 or more pulses per second without going into immediate tetany. In *Bagre*, the frequency response of the sonic system is about an octave higher than that in *Galeichthys*.

Spontaneous sounds from these species consist of low-pitched grunts (fundamental pitch of about 150 cycles per second) and, in *Bagre*, higher, sob-like sounds (400 cycles per second or over).

The harmonic components of both artificially induced and spontaneous sounds can be influenced by the amount of sound reflectance in the external environment. Even under partially anechoic conditions, the sound output is virtually a pure tone. Damage to the swim bladder reduces the amplitude of the sound but not its timbre (i.e., harmonic content). It was concluded that the swim bladder does not serve as a resonating chamber for these sounds, nor is it a true amplifier. Rather, it transfers the energy from the small area of the vibrating Müllerian ramus to the larger area of its entire outer surface, thus making the propagation of the sound from its source to the water more efficient. In acoustical and electronic terms, the swim bladder is an impedance matching device.

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