PALEOPSEPHURUS WILSONI, A NEW POLYO-DONTID FISH FROM THE UPPER CRETA-CEOUS OF MONTANA, WITH A DISCUSSION OF ALLIED FISH, LIVING AND FOSSIL

BY

ARCHIE MacALPIN

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INTRODUCTION

IN THE summer of 1938 an expedition from the Museum of Paleontology of the University of Michigan excavated a large trachodont from the Upper Cretaceous Hell Creek beds at a

point about twenty-four miles southeast of Fort Peck, Montana. During the work portions of three fish were recovered. All available material was brought to the Museum of Paleontology for study. Examination showed that one of the specimens consisted of part of the head and most of the body of a completely scaled sturgeon-like fish superficially resembling *Scaphirhynchus*.

Within eighteen inches of this specimen were found the complete head skeleton, associated pectoral girdle, and pectoral fins of another fish belonging to the Polyodontidae. In a block of matrix from the same spot there were later discovered a portion of the caudal region of one fish and the posterior part of the shoulder girdle possibly belonging to another, both of which are of the same species of polyodontid as that represented by the complete head. Since it is impossible to determine whether the fish illustrated by the caudal region was also the owner of the complete head or of the fragment of shoulder girdle or of neither, each incomplete part will be regarded as belonging to a separate individual.

The Scaphirhynchus-like acipenseroid (22210 U.M.) from Montana will be described at a later time. This paper will deal principally with fossil and living polyodontids.

In spite of their strongly chondrostean characters the Recent Polyodontidae have many features that are sharklike in their simplicity (Bridge, 1878; Sewertzoff, 1923, 1926, 1928; Regan, 1904; Tatarko, 1937). An almost complete lack of paleontological and embryological material leaves the background of this interesting group much in the dark. Therefore the morphology of a remarkably well preserved head and part of the body of a Cretaceous paddlefish is of great interest.

It is the purpose of this paper to make a contribution to the knowledge of the comparative morphology of the Polyodontidae and, if possible, to indicate evolutionary trends within the family. It is also the aim to review the fossil material ascribed to the Polyodontidae and to note several structures hitherto undescribed in Recent forms.

The specimens from Montana here described and Cope's *Crossopholis* were studied from the actual material. The Mon-

tana fossils are embedded in a sandstone made up principally of sharply angular grains of quartz and fragments of limonite containing much silica. There is also some fresh and altered albite. These are cemented together with calcite and kaolin minerals. For a description of the beds from which this material came see a paper by Barnum Brown (1907, p. 832).

The matrix overlying the bone was removed with needles under a binocular microscope. Alteration has largely destroyed the internal structure of the bone. Much of the bone was so delicate that it had to be hardened as cleaning progressed.

The ends of certain bones not easily accessible were exposed by a vertical break that occurred diagonal to the median plane of the cranium. The matrix on the surface of the fracture was painted with Chinese white water color to make the position of the bones more obvious (Pl. IV, Figs. 1–2).

In the course of the work preserved and fresh specimens of *Polyodon, Scaphirhynchus, Acipenser,* and *Psephurus* were inspected and compared with the fossil material.

PREVIOUS WORK

Literature on fossil polyodontids is extremely meager because of almost complete lack of material. References to modern forms are more abundant and, with a few exceptions, are brief and widely scattered.

In 1883 Cope first described the posterior part of the body of *Crossopholis magnicaudatus,* an Eocene polyodontid from the Green River shales of Wyoming. In 1886 he described and figured the skull of a second specimen of the same species, and redescribed and figured the type. Woodward, who described *Pholidurus disjectus* from the Cretaceous chalk of England in 1889 and 1909, believed it to be polyodontid in character. Both *Crossopholis* and *Pholidurus* have been mentioned in many texts on paleontology, but no additions to the descriptions have been made.

Polyodon spathula (Walbaum), the modern Mississippi paddlefish, remained in uncertain taxonomic position from the time it was first described as *Squalus spatula* by Maduit in 1774 until

it was recognized as a ganoid in 1846 by Müller, who established the suborder Chondrostei for its reception. In 1877 Part I of Traquair's *Ganoid Fishes of the British Carboniferous Formations* was published. It contains excellent figures showing the skeleton of the head of a *Polyodon*, jaws, pectoral girdle, and fins, and the external appearance of the tail. Traquair pointed out the close relationship between the palaeoniscids and the polyodontids and described several structures in the latter not previously recognized.' In 1878 Bridge published the first comprehensive osteology of *Polyodon*, with many figures and comparisons with other forms. ' Other important contributions are those of Allis (1903) on ' the lateral sensory canals and cranial bones, Allis (1911) on the pseudobranchial and carotid arteries, Danforth (1912) on the ' heart and arteries, Danforth (1913) on the myology, Norris (1925) on peripheral distribution of cranial nerves, and Allis (1935) on the cranial roofing bones. For bibliographies of the vast number of papers containing less important references to *Polyodon* see Bridge (1878), Dean (1916–23), Hay (1929), Goodrich (1930), and Holly (1936). The literature cited at the end of this paper contains some newer publications not listed by *?* the authors here mentioned.

   Psephurus gladius (Martens), the modern Chinese paddlefish, has received scant attention in the literature. It was first described by Martens (1862) as *Polyodon gladius* and recognized as a separate genus by Günther (1873). Regan (1904) figured . and described the skeleton of the anal, pelvic, and pectoral fins ˉ in his discussion of the affinities of the Chondrostei. Tatarko (1937) treated the visceral arches, together with those of *Polyodon.* ˋ For further references to *Psephurus* see the publications listed · above.

   An abstract of this paper appeared in the *Bulletin of the Geological Society of America* in December, 1941 (MacAlpin, 1941).

of the Museum of Zoology, has been most kind in securing fresh and preserved material for dissection. I wish to thank Dr. Leonard P. Schultz, of the United States National Museum, for donating a specimen of *Psephurus* to the Museum of Zoology for my use and for permitting me to examine the remaining specimens in the National Museum. I am indebted to the American Museum of Natural History in New York for the loan of the original specimens of *Crossopholis*. Plates I, II, and III are from photographs taken by Dr. Case; Plate IV is from photographs by Dr. Laurence C. Stuart, of the Department of Zoology, University of Michigan.

Material. — (1) A single well-preserved head (22206 U.M.), complete with the jaws and branchial arches, pectoral girdle, pectoral fins, and some minute denticles. (2) A portion of the caudal region of a second specimen (22207 U.M.). (3) A posterior fragment of shoulder and associated pectoral fin of a third specimen (22208 U.M.).

General description. — *Paleopsephurus wilsoni* is closely related to the Recent *Psephurus gladius* and *Polyodon spathula*, and belongs to the family Polyodontidae. It has a long rostrum, a fenestrated cranial roof skeleton with numerous bony plates in the occipital region, and a large mouth placed well back under the otic region and supported by a strongly oblique suspensorium. It has a quadratojugal, a well-developed subopercular, and a dermal shoulder girdle. Investing bones of the chondrocranium are only weakly developed. The trunk is covered with small spinous denticles, not in contact. Caudal fulcra and caudal oat-shaped scutes are present.

Chondrocranium and Its Investing Bones

The chondrocranium was undoubtedly of massive proportions, as it is in the living chondrosteans. No trace of cartilaginous remains could be made out.

There is a small investing bone of the chondrocranium that appears to be the opisthotic, although its position indicates that

it may contain part of the proötic as well (Pl. IV, Figs. 1–2, OPIS). Its general outline is indicated by a distinctive brown color preserved in the matrix and by actual granules of bony material.

The opisthotic is roughly round, being about 0.8 cm. in diameter. The surface facing medially, anteriorly, and somewhat dorsally is shallowly concave. Its medioventral edge lies in contact with the dorsal surface of the parasphenoid near its lateral edge. The most anterior point of this contact is about a centimeter behind the posterior edge of the ascending ramus of the parasphenoid. The laterodorsal edge overlies the hyomandibular near its head.

Part of the opisthotic is exposed in the plane of the vertical fracture that crosses the specimen in such a way as to cut through the head of the right hyomandibular and the base of the left one. When the matrix was freed from the lateral surface of the right opisthotic, an area in the center appeared to be entirely devoid of bone. If this is a foramen, it has the correct position, when compared with modern forms, to be that for the vagus nerve (Pl. IV, Fig. 2, VF). In more aged specimens of *Polyodon* an extremely thin ectosteal plate lies on the chondrocranium just dorsal and anterior to the foramen for the vagus nerve (Bridge, 1878, p. 698; Pl. 55, Fig. 3; Pl. 57, Fig. 7). This bone could not be found in the specimen of *Psephurus* that was examined, a condition which may be due to its youth. Parker (1882) described several ossifications, including one that he called the proötic, embedded in the chondrocranium of a very old *Acipenser sturio*. Holmgren and Stensiö (1936) show in *Acipenser güldenstaedti* a small triangular ossification lying just anterior to the vagus foramen. This they call the opisthotic, and it appears to be homologous with the opisthotic of *Paleopsephurus wilsoni*. In *Hypsocormus*, an Upper Jurassic holostean, and in the living *Polypterus* the vagus nerve escapes through a foramen in the opisthotic; in *Amia* the opisthotic, together with the lateral occipital, enclose the foramina for the vagus. Allis (1899) was convinced, however, that the so-called opisthotic in *Amia* is of membranous origin.

There is a thin splint of bone about 2.5 cm. long that, because of its relationship to the opisthotic and its probable relationship to the chondrocranium, will be described here, although it may possibly be of dermal origin. Its true homologies are uncertain, and it is here called "epiotic" (Figs. 1–2; Pl. IV, Figs. 1–2, "EPI") merely as a convenient way of designating its topo-graphic position. A section transverse to its length has the shape of an inverted L, with the vertical stem directed ventrally and the horizontal stem directed posterolaterally. The epiotic is closely applied to the ventral surface of the intertemporal. It extends medio-postero-dorsally from a point beneath the inter-temporal's center of ossification, crosses the posterior division of the fenestra longitudinalis obliquely, passes about 0.2 cm. ventral to the parietal, and ends freely about 0.5 cm. from the midplane of the cranium. It lies in the same vertical plane as the opisthotic, and its ventral edge lies within 0.1 cm. of the latter's dorsal edge.

In *Psephurus* and *Polyodon* the cartilaginous labyrinth region of the chondrocranium expands outward from the occipital region in a position comparable to that occupied by the epiotic of *Paleo-psephurus*. In the recent forms part of the m. retractor hyomandi-bularis (Danforth, 1913) originates from this area (Figs. 4–5, M.RHM), and it seems likely that the epiotic of *Paleopsephurus* furnished an area for a similar muscular origin.

Dermal Roofing Bones of the Chondrocranium

Unfortunately, much of the bone of the roof posterior to the rostrum was lost. The general pattern could be worked out, however, with reasonable certainty because fragments of bone were left here and there, particularly in the lateral and posterior areas, and wherever the bone was missing, a characteristic brown stain and a fairly decipherable impression remained in the matrix. Radiating lines from the centers of ossification can be seen on this mold and on the undestroyed bone fragments. The postrostral sutures indicated in the restorations in Figures 1 and 2 undoubtedly do not conform exactly to those that would be seen if the bones were complete. If the better-preserved right extrascapular region
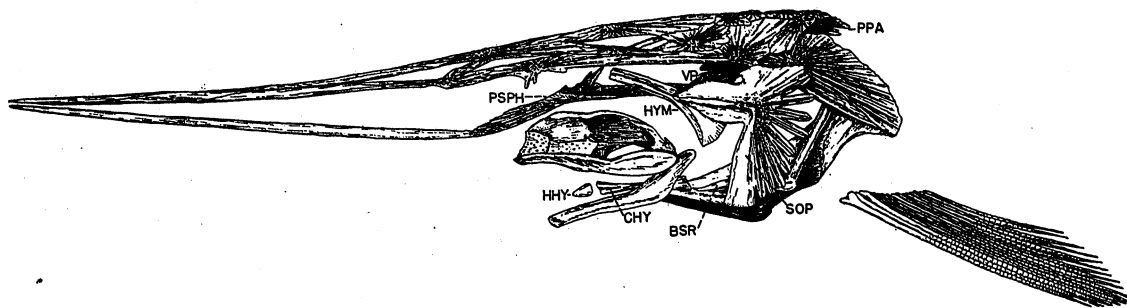
FIG. 1. *Paleopsephurus wilsoni,* No. 22206 U.M.   Restoration

Abbreviations: BSR, branchiostegal rays; CHY, ceratohyal; HHY, hypohyal; HYM, hyomandibular; PPA, posterior extension of the parietals; PSPH, parasphenoid; SOP, subopercular; VP, ventral process of the extrascapular. $\times \frac{2}{5}$

represents a condition that was prevalent over the entire roof of the skull, then it may be concluded that the articulations were strongly overlapped and somewhat interfingered. Except for the fenestrations present in *Paleopsephurus* the roofing bones form a shield more like that of Recent acipensers than that of Recent polyodons.

The usual difficulty that arises as the result of disagreement among previous authors in determining the bones of the head is present here. Stensiö (1921, 1925, 1932, and other papers), Säve-Söderbergh (1933), and, to some degree, Allis (1935) have adopted a system whereby each bone believed to be composed of several previously distinct bones bears a compound name derived from the contributing bones. In spite of certain objections the system will be used in this paper, with some of the modifications suggested by Allis (1935).

The occipital region of *Paleopsephurus* is roofed by several close-
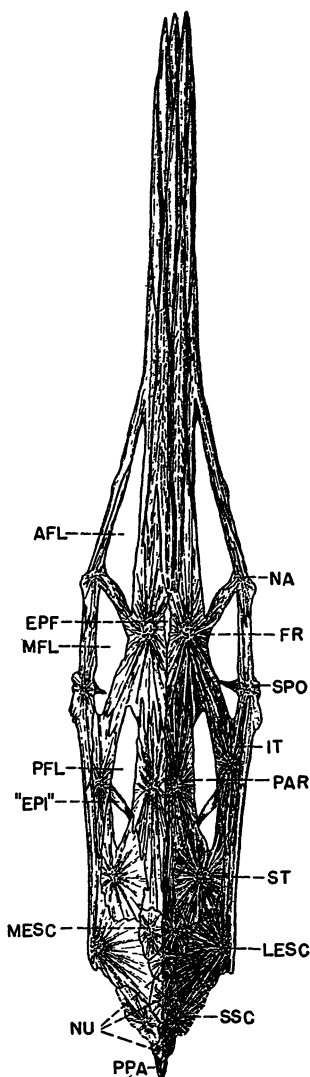
FIG. 2. *Paleopsephurus wilsoni*, No. 22206 U.M. Restoration

Abbreviations: AFL, anterior division of the fenestra longitudinalis; EPF, epiphyseal fenestra; "EPI," "epiotic"; FR, frontal; IT, intertemporal; LESC, lateral extrascapular; MESC, median extrascapular; MFL, middle division of the fenestra longitudinalis; NA, nasal; NU, nuchals; PAR, parietal; PFL, posterior division of the fenestra longitudinalis; PPA, posterior extension of the parietals; SPO, suprapostorbital; SSC, suprascapular; ST, supratemporal. × ½

sutured bony plates in the way characteristic of the living sturgeons but lacking in the living paddlefish. Posteriorly there is a series of three or possibly four unpaired median elements (Fig. 2, NU). Their exact boundaries cannot be determined, but enough fossil material remains to indicate that these bones are roughly oval and that they overlap posteriorly. A single bone or several bones similarly placed in *Acipenser* are sometimes referred to as postoccipitals (Goodrich, 1930; Sewertzoff, 1926; Gregory, 1933). The bone immediately anterior to the so-called postoccipital is called the "supraoccipital" by Goodrich (1930) and the "dermosupraoccipital" by Sewertzoff (1926) and Gregory (1933). Since the term "supraoccipital" has been abandoned in this paper for reasons suggested by Allis (1935), it seems best to avoid the use of the term "postoccipital" as well and to refer to the posterior series of bones in *Paleopsephurus* as the "nuchals," according to the usage of Luther (1913), Gegenbaur (1898), and Kurz (1924) for the apparently homologous bones in the sturgeons. The character of the nuchals suggests that they are the anterior representatives of what may have been a more complete row of dorsal ridge scutes in some form ancestral to *Paleopsephurus*. Such a dorsal series is present in Recent sturgeons and at least some of the fossil *Saurichthys* (Stensiö, 1925, p. 95, and text figs. 20, 45, 46). Jaekel (1929, Fig. 20) shows a similar series in the crossopterygian *Glyptopomus*.

Immediately anterior to the nuchals is a pair of small irregularly oval median extrascapulars (Fig. 2, MESC). They are suturally united throughout most of their length and overlap the most anterior nuchal. So far as can be made out from the condition of the specimen, they appear to be bounded by the parietals anteriorly and ventrally (cf. the description of the parietals in the paragraph below), by the supratemporals laterally and anteriorly, and by the lateral extrascapulars laterally and somewhat posteriorly. In most of the chondrosteans the median extrascapulars are paired, but in *Acipenser* they are sometimes fused into a single bone, as shown by Sewertzoff (1928).

The visible part of each of the parietals (Fig. 2, PAR) is long and subrectangular, and the two bones are joined suturally

throughout their length. The anterior part of the lateral edge of each marks the inner boundary of the posterior division of the fenestra longitudinalis (Allis, 1935). It is uncertain whether the parietals were partly hidden in a dorsal view by the supratemporals meeting in midline or whether their exposed surfaces continued posteriorly to the median extrascapulars. From the appearance of the specimen and from the condition that exists in related fish the second state appears to have been true. The parietals do not end posteriorly at the median extrascapulars, but continue beneath them and the nuchals as a pair of juxtaposed splints forming a median keel.

The center of ossification of each parietal is at a distance from its anterior end equal to one quarter of the entire length of the bone. The median keel, mentioned above, begins about 2 cm. behind the center of ossification and gradually increases to a height of 0.8 cm. at its posterior end, where it protrudes beyond the last nuchal preserved (Figs. 1–2, PPA). In a sturgeon that was examined the parietals extend beneath the median extrascapular and the nuchal as broad thin splints. Although the median extrascapulars and nuchals are lacking in the Recent paddlefish, the parietals extend backward well over the spinal column, and there is a suggestion of a shallow keel posteriorly.

Each of the frontals (Fig. 2, FR) in *Paleopsephurus* is securely joined posteriorly to the anterior end of the corresponding parietal by an interfingering suture. The frontal is long, narrows slightly anteriorly, and has its center of ossification at about the center of the bone. The posterior half of each joins its fellow in the midline, but there is a small fenestra separating the bones opposite their centers of ossification (Fig. 2, EPF).

The exact width of this fenestra is indeterminable because some loss of bone in that area obliterated the outline. In *Polyodon* the union of the parietals along the midline may be interrupted in as many as three places (Jaekel, 1929, pl. 3, fig. A). One of the specimens available has two fairly large openings. The anterior one exposes the anterior median fontanelle (Bridge, 1878). In the specimen of *Psephurus* the parietals are united opposite their centers of ossification and are somewhat separated posteriorly.
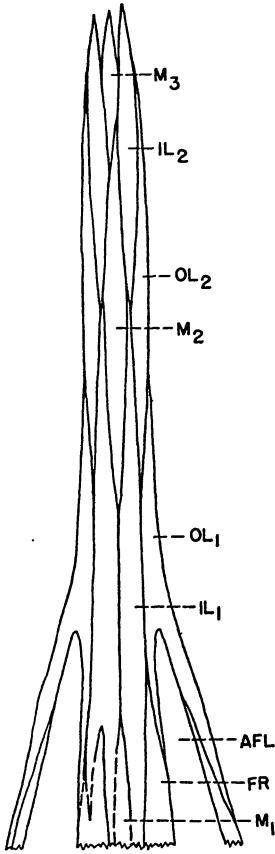
In it the anterior median fontanelle is
not visible. The interparietal fenestra
has been called both the "pineal" and
the "epiphyseal" (Luther, 1913; Allis,
1935). In *Sinusturio* (Kurz, 1924;
Jaekel, 1929), one of the least ossified
sturgeons, a broad fenestra exposes the
chondrocranium between the frontals
for their entire length and even extends
between the anterior ends of the pari-
etals. Jaekel calls this the "*Epiphysen-
fenster.*" In the more highly ossified
acipensers and in *Scaphirhynchus* there
are a variable number of small plates
between the frontals lying superficial
to the dorsal end of the epiphyseal
fossa which are generally called the
"epiphysalia" (Luther, 1913; Jaekel,
1929; Allis, 1935), but which Sewertzoff
(1926) regards collectively as the pos-
terior median dorsorostral.

Lateral to the center of ossification
each frontal of *Paleopsephurus* sends
a process anterolaterally that partly
crosses the anterior division of the fe-
nestra longitudinalis and meets a similar
process directed posteromedially from
the nasal. More will be said about
these processes in the section where
the possible course of the laterosensory
canals is discussed (see pp. 184–185).
In front of this process the outer edge
of each frontal marks the posterior half
of the inner boundary of the anterior

division of the fenestra longitudinalis. Behind this process the outer edge of each frontal forms the boundary of the broad apex of the triangular middle division of the fenestra.

Posteriorly the frontal is divided into two arms enclosing the anterior tip of the posterior division of the fenestra longitudinalis. The medial arm is united by a suture to the anterior end of the parietal, as mentioned above. The posterolaterally directed arm is articulated suturally with a similar process directed antero-medially from the intertemporal.

Directly anterior to the epiphyseal fenestra there is some indication of a lenticular element that, if present, would be the posterior median dorsorostral (Fig. 3, M_1).[1] The broken condition of the bone does not allow a conclusive determination of this. Since, however, there exists a single bone or a pair of bones (Luther, 1913, fig. 4 of *Acipenser ruthenus*) in a comparable position in many ganoids, especially those closely related to *Paleopsephurus*, its presence is probable. In *Polyodon* and *Acipenser* the M_1 bone has been called the "dermomesethmoid" by Luther (1913), the "dermoethmoid" by Bridge (1878), and one of the postrostral splints by Holmgren and Stensiö (1936). The term used here is the one employed by Allis (see footnote below).

Anterior to M_1, but separated from it by the meeting of the posterior inner lateral dorsorostrals (IL_1), are two more median dorsorostrals (Fig. 3, M_2 and M_3). These are spindle-shaped and are in contact by a slight overlap at their adjoining tips. M_2 is about two and one-half times the length of M_3. In *Polyodon* there are at least four median dorsorostrals.

[1] The nomenclature adopted by Allis (1935) defines the positions of the dorsorostral bones more accurately than that of Bridge (1878). As will be seen, Allis' terms are sometimes extremely long and difficult to handle in descriptive material. In this paper a dorsorostral bone will be first introduced by Allis' term and subsequently referred to by a convenient symbol.

Allis' terms	Bridge's symbols	Symbols used here
Posterior median dorsorostral..........	a^1	M_1
Anterior median dorsorostrals..........	a^2 and a^3	M_2 and M_3
Posterior inner lateral dorsorostral.....	b^3	IL_1
Anterior inner lateral dorsorostrals.....	b^4 and b^5	IL_2
Posterior outer lateral dorsorostral.....	c^3	OL_1
Anterior outer lateral dorsorostrals.....	c^4 and c^5	OL_2

A pair of posterior inner lateral dorsorostrals (Fig. 3, IL_1) are joined posteriorly to the anterior ends of the frontals by W-shaped sutures. They are separated along their posterior third by M_1, joined along their middle third by a suture and separated along their anterior third by M_2. Each IL_1 gradually tapers forward to a fine point, which extends between M_2 and OL_2 for half of their length.

The anterior inner lateral dorsorostrals (Fig. 3, IL_2) extend from the anterior tips of the IL_1 bones for a distance equal to half their lengths. These are characteristically spindle-shaped and are separated by M_2 and M_3.

In the occipital region there are found a pair of almond-shaped bones that are interpreted as the suprascapulars (Fig. 2, SSC). The long axis of each extends forward, downward, and outward. Medially they are in contact with the most posterior nuchal; anteromedially, with the middle nuchal and lateral extrascapulars. Their posterolateral edges were broken and could not be traced exactly. The boundary between the smooth and the ridged parts of the anterior end of the supracleithrum was used to determine the possible posterior extent of each suprascapular and is indi-cated in Figures 1 and 2 by a dashed line.

The bones that lie on the posterolateral corners of the cranial roof (Fig. 2, LESC) are of considerable interest. Each consists of a main body that faces dorsolaterally, a long anterior extension of the lateral edge that forms the lateral boundary of the dermal roof, a short posterior extension that curves somewhat ventrally, and a ventral process, which will be described in detail on pages 181–182.

The bone on each posterolateral corner of the cranial roof in *Polyodon* has been referred to by various authors as the squamosal (Traquair, 1877), posttemporal (Bridge, 1878; Collinge, 1894), supraclavicular (Allis, 1903), frontal (Danforth, 1913, fig. 6, al-though this must have been a typographical error), supratemporal externum (Luther, 1913), extrascapular (Stensiö, 1925; Holm-gren and Stensiö, 1936), postoccipital (Jaekel, 1929), pterotic (Goodrich, 1930; Holly, 1936), and extrascapulo-suprascapular (Allis, 1935). Because it appears that *Paleopsephurus* has a

separate suprascapular and median extrascapular, the bone will be called the "lateral extrascapular" (Fig. 2, LESC).

The edge of the main body of the lateral extrascapular is over-lapped by the edges of all the bounding roofing bones. The supratemporal lies in the angle between the anteromedial edge and the forward lateral extension. The median extrascapular bounds at least the inner half of the posterior margin. The center of ossification is close to the lateral edge, about a centi-meter anterior to the posterolateral corner. The bone is stouter than the other roofing bones, and at its center of ossification is about 0.3 cm. thick. The lateral edge is thickened and rounded. The anterior extension along the lateral edge is bounded medially by the supratemporal, as mentioned above, and anteriorly by the intertemporal. The anterior end of this extension lies in sutural contact with the posterior end of the suprapostorbital.

On the ventral surface of the lateral extrascapular near its lateral edge a short thin posterior extension of unknown function originates under the center of ossification and curves gently back-ward and downward.

The ventral process of the lateral extrascapular has a dorsal and a ventral component. (See Fig. 1, VP, and Pl. IV, Figs. 1–2, VVP and DVP.) The dorsal component has the shape of a vertical flange attached to the ventral surface of the main body of the bone. It extends in a medio-antero-dorsal direction from the lateral edge beneath the center of ossification to a point almost in the median plane of the cranium. The medial half of the dorsal flange is about 0.3 cm. in height. From its lateral half the ventral component extends as a thin plate about a centime-ter high, lying in a medio-antero-ventral direction. This ventral plate is 1.8 cm. long and medially concave in a section trans-verse to its long axis. Its inwardly curved ventral edge lies for half its length in contact with the dorsal surface of the para-sphenoid near its lateral edge.

Both the acipensers and the polyodons have structures homol-ogous with the ventral process of *Paleopsephurus*. In the acipen-sers it is less well developed. In *Polyodon* and *Psephurus*, on the contrary, it is much more extensive in length and height than in

Paleopsephurus. The relationship that the ventral process bears
to the trunk muscle will be discussed in the section that compares
Paleopsephurus with other fish (pp. 225–226).

The Triassic fish *Wimania*, a coelacanthid, and *Birgeria* and
Saurichthys, palaeoniscids, bear ventral processes from the pos-
terolateral corners of the cranial roof. In spite of the marked
similarity of these processes to the ones of the Polyodontidae
Stensiö (1925) does not believe them to be homologous. He says
(1925, p. 218): "In the Saurichthyids there is no equivalent to
the process that, in Acipenserids and Polyodontids, descends from
the extrascapular on the anterior side of each cranio-spinal process;
but this process is also lacking in Palaeoniscids and appears to
be absent in other primitive Actinopterygians too. Consequently
it seems most probable that its presence in Acipenserids and
Polyodontids is to be considered as a rather late specialization."

The supratemporal (Fig. 2, ST) overlies the anteromedial edge
of the lateral extrascapular. It is broadly oval, with its long axis
extending in an anterior direction. Anteriorly the supratemporal
has a deep notch that forms the posterior boundary of the posterior
division of the fenestra longitudinalis. Its medial edge overlies
the parietal, and its posteromedial edge the median extrascapular.
The lateral edge lies in contact with the intertemporal.

The intertemporal of *Paleopsephurus* (Fig. 2, IT) is an arrow-
shaped bone with the point directed backward. This point is
inserted between the supratemporal medially and the lateral
extrascapular laterally. The boundary of the lateral border is
completed anteriorly by the posterior half of the medial border
of the suprapostorbital. The anterior part of the medial edge
marks the outer boundary of the posterior division of the fenestra
longitudinalis. An anteromedially directed arm is united with a
posterolaterally directed arm from the frontal by a strongly inter-
fingered suture. The anterior edge is shallowly notched by the
posterior end of the middle division of the fenestra longitudinalis.

The suprapostorbital (Fig. 2, SPO) forms the edge of the
cranial roof between the anterior lateral process of the lateral
extrascapular and the posterior end of the nasal. It is a com-
paratively narrow, stout splint whose center of ossification lies

halfway between its ends. Its inner edge forms the outer boundary for the middle division of the fenestra longitudinalis. On the lateral edge, opposite the center of ossification, there is a slight ventral expansion of the bone that bears two small finger-like processes. Immediately posterior to this expansion lies another, which is more lateral in position and bears no finger-like processes. There is also a horizontal styliform process extending inwardly from the center of ossification to a point lying a little medial and ventral to the outer edge of the frontal (Fig. 1).

The nasal bone (Fig. 2, NA) lies anterior to the front end of the suprapostorbital and is united to it by a strong suture. It is made up of three arms joined at the center of ossification. A short arm, directed posteriorly, is united to the suprapostorbital; a second short arm, directed posteromedially, is joined to the anterolateral process from the frontal; the third and longest arm, directed anteriorly and a little medially, articulates by its lateral surface to the medial surface of the lateral arm of OL_1.

There are two outer lateral dorsorostrals on each side of the rostrum (Fig. 3, OL_1 and OL_2). The posterior of these, OL_1, has the shape of an elongate Y, with the stem directed anteriorly and with the anterior end of the anterior division of the fenestra longitudinalis lying between the posteriorly directed arms. Its lateral arm is joined medially to the nasal by a long suture. The medial arm and the stem form a fairly straight medial surface, the posterior quarter of which joins the frontal; the middle half joins IL_1 and the anterior quarter joins OL_2. This bone last mentioned, together with a small tip of IL_3, completes the lateral edge of the rostrum.

In *Paleopsephurus* there is no trace preserved of any stellate bones such as are developed so strongly in *Polyodon* to support the lateral extensions of the "paddle" or such as are developed to a less degree in *Crossopholis* and *Psephurus*.

Ornamentation on the roofing bones. — Wherever fragments of the cranial bones could be observed, they were strongly sculptured in the form of sharp ridges and grooves radiating from the centers of ossification (Figs. 1–2). These centers are marked with nodes and short irregular ridges. This is fairly well shown on the

right lateral extrascapular and on a small fragment of bone that had lodged in a hole broken in the skull just anterior to the left median extrascapular and thus had been preserved. The ornamentation resembles that of the recent Acipenseridae rather than that of the Polyodontidae.

The rostral bones are well preserved. Each shows a low central ridge throughout its length. On the posterior two thirds of each IL_1 bone each side of the ridge is decorated with shorter ridges directed anteromedially *en échelon.*

Laterosensory Canals and Homologues of Related Bones

The alteration or complete destruction of the cranial roofing bones in *Paleopsephurus* was such that the attempt to determine definitely any remains of the laterosensory canals was unsuccessful. Thus the terminology used in this paper is not meant to imply conclusive proof that the bones were either overlain or penetrated by the laterosensory canals. The similarity of the roofing pattern to that of *Polyodon,* and to some degree to that of other forms, indicates that the laterosensory canals followed similar courses. Detailed descriptions of the laterosensory canals of *Polyodon* will be found in Collinge (1894), Allis (1903, 1935), and Holmgren and Stensiö (1936).

In *Crossopholis magnicaudatus* the main laterosensory canal of the trunk was enclosed in a closely packed series of small perforated bony discs (Fig. 23, MLS). They are well preserved in both specimens. The canal approaches the supracleithrum in such a way as to pass through or across its dorsal end, although no trace of it could actually be found in the bone itself.

The supracleithrum of *Paleopsephurus* is relatively wider than it is in the other polyodontids. The laterosensory canal probably pierced it in a more ventral position with respect to its dorsal edge. From there it must have entered the posterolateral part of the suprascapular, and continued forward through, or across, the lateral extrascapular and supratemporal until it reached the central part of the intertemporal. The supratemporal commissure branch probably came off medially from the main canal somewhere near the center of ossification of the lateral extrascapular and ap-

proached or met a similar branch from the opposite side near the midline suture of the median extrascapulars.

In *Paleopsephurus* the condition of the intertemporal portion of the canal must have been much the same as that in *Polyodon*. According to Allis (1935, p. 237), the bone here called the intertemporal of *Polyodon* "thus represents in topographical position and in its relations to the latero-sensory canals a latero-sensory sphenopterotic portion of the membranous outer lateral dorsocranial (suprapostorbital) and these two bones, if fused with each other, would form the two components of the dermosphenopterotic comparable to that described by me [Allis, 1905] in *Lepidosteus* but there called the squamosal." But the bone referred to here as the suprapostorbital also contains a dermal component developed in conjunction with the sphenotic process of the chondrocranium. Hence the use of the terms "supratemporal" and "intertemporal" (as suggested by Holmgren and Stensiö, 1936) seems the simplest way of describing the condition in *Paleopsephurus*, in spite of the controversy regarding their appropriateness (Allis, 1935). The name "dermopterotic" for the supratemporo-intertemporal, used by some to avoid this controversy (for example, Westoll, 1937b), leaves unnamed the posterior element in *Paleopsephurus* that lies well behind the pterotic region of the chondrocranium.

Allis (1935) has carefully shown that the suprapostorbital of *Polyodon* is made up of components from the supraorbital, the postorbital, and the membranosphenotic, and thus it should be called the suprapostorbito-membrano-sphenotic. It also overlies the pterotic ridge of the chondrocranium (Bridge, 1878), so that probably the term "pterotic" should be added. To avoid this awkward term Allis simply calls the bone the outer lateral dorsocranial. Holmgren and Stensiö (1936) confirm Allis' view regarding the components of this bone, but to avoid the long name adopt the term "postfrontale." The name "suprapostorbital" is suggested here because it fairly indicates the bone's topographic position and avoids the controversial "postfrontal" and the double application of "sphenotic" and "pterotic."

Bridge's description and figures of the bone b[3] (cf. note, p. 179 of this paper), lying anterior to the frontal, and c[3], anterior to

the suprapostorbital in *Polyodon*, are somewhat difficult to interpret. Collinge's figure (1894) is obviously in error. In a *Polyodon* 89.5 cm. long the anterior end of the suprapostorbital is suturally interfingered with a series of six or seven small closely joined splints that, if taken together, occupy a position similar to that of the nasal in *Paleopsephurus*. The supraorbital laterosensory canal passes dorsal to this suture. The bones in *Polyodon* and *Psephurus* corresponding to OL_1 in *Paleopsephurus* are of much the same shape in the three fish. In *Polyodon*, however, the nasal articulates with OL_1 by its medial edge; in *Psephurus*, by its lateral edge. The specimen of *Psephurus* was so small (36 cm.) and the splints were so irregularly developed in the nasal region that it was difficult to determine any true boundaries. Furthermore, because it was to be preserved in the Museum of Zoology of the University of Michigan it could not be more completely dissected. The adult *Psephurus*, which may attain four feet in length, would undoubtedly show many features of great morphological interest.

The suture of the posteromedially directed arm of the nasal and the anterolaterally directed arm of the frontal is ill defined in *Paleopsephurus* (Figs. 1–2), but there appears to be a definite extension of bone from each to form a bar over the fenestra longitudinalis. This strongly developed bar was either pierced by, or was ventral to, the supraorbital laterosensory canal as it descended in an arc over the frontal. The position of the frontonasal bar and the greater extension of the posterolaterally directed arm of the frontal show that the supraorbital canal extended more medially over the frontal than it does in *Polyodon* or *Psephurus*.

There were no laterosensory canal ossicles preserved in *Paleopsephurus* that could be definitely determined as belonging to the series that continues the supraorbital or the infraorbital canals into the dermis.

Ventral Rostrocranial Skeleton

The parasphenoid (Figs. 1, 5, PSPH; Pl. IV, Fig. 1) is accessible to ventral view anterior to the diagonal fracture previously mentioned. It is considerably broader and stouter than in *Polyo-*
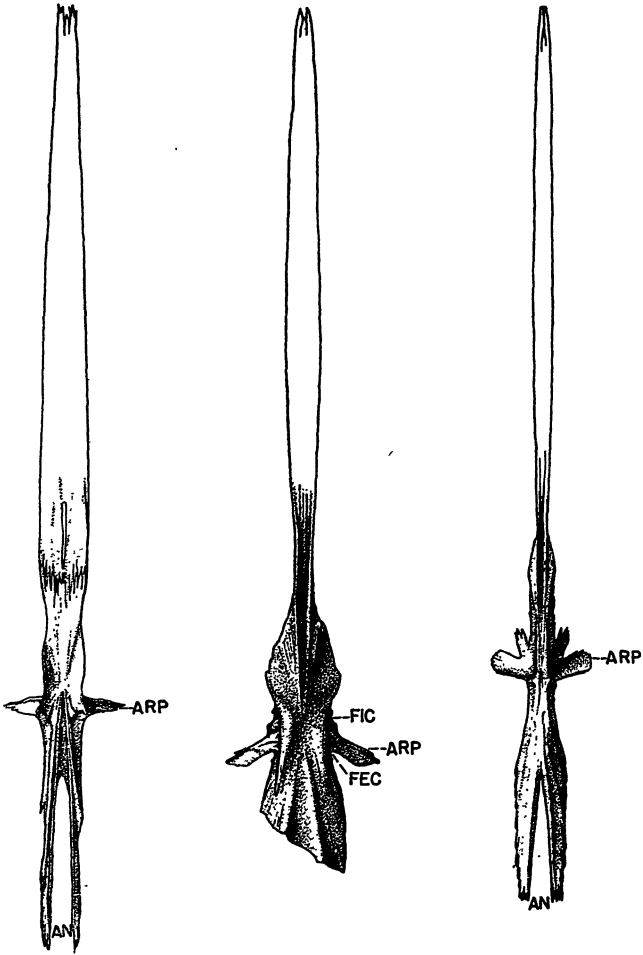
FIG. 4   FIG. 5   FIG. 6

FIG. 4. *Polyodon spathula*. Parasphenoid from a ventral view. × ⅓
FIG. 5. *Paleopsephurus wilsoni*, No. 22206 U.M. Anterior portion of
the parasphenoid from a ventral view. × ½
FIG. 6. *Psephurus gladius*. Parasphenoid from a ventral view. × ½

Abbreviations: AN, aortic notch; ARP, ascending ramus; FEC,
position of the external carotid foramen; FIC, position of the in-
ternal carotid foramen.

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don and *Psephurus*. The parasphenoids of the three fish resemble
one another in general appearance, but are notably different in
detail (cf. Figs. 4–6).

It is reasonably certain that the posterior part of the bone that
is buried in the matrix is deeply notched from behind and that
the two wings thus formed extend posteriorly well beyond the
occipital region. In the living acipenserids and polyodontids
these wings are applied along the ventrolateral surface of the
notochord, and between their medial edges lies the dorsal aorta
(Figs. 6, 8, AN). It is held that this condition is true in the fossils
Birgeria (Stensiö, 1921), *Chondroteus* (Watson, 1928), and *Sau-
richthys* (Stensiö, 1925).

The parasphenoid and the "prevomers," or at least the sub-
rostral elements next anterior to the parasphenoid, must have
been very closely united in *Paleopsephurus*, because the suture
is not at all evident in the specimen. This may be partly due to
the somewhat broken condition of the bone. It is clear, however,
that the suture did not lie posterior to the anterior end of the jaws.
A similar condition in *Polyodon* led Allis (1919) to doubt the accu-
racy of calling these posterior subrostral bones the vomers. If the
parasphenoid-"prevomer" suture occupied a position in *Paleopse-
phurus* similar to that in *Polyodon*, it occurred in the region of the
greatest down-arching of the entire ventral rostrocranial support.

The center of ossification of the parasphenoid in *Paleopsephurus*
is at a point defined by the intersection of lines continuing the
anterior edges of the ascending rami. Fine plicae fan out forward
and backward from this center (Pl. III, Figs. 1–2). Posterior
to the center of ossification the axial line of the parasphenoid lies
horizontally; anteriorly it swings downward and forward and
then, as continued by the subrostral elements, slopes gently up-
ward to the end of the snout (Fig. 1, PSPH). This shape is
similar to that found somewhat less markedly in *Psephurus*. In
Polyodon the entire ventral rostrocranial support lies in an almost
horizontal plane. The strong arch present in this region in *Paleo-
psephurus* and *Psephurus* may be related to the character of the
hyomandibular muscles and the jaw movement. This possibility
will be considered later (p. 225).

For the purpose of description the main body of the para-
sphenoid may be assumed to be made up of an anterior division
and a posterior division, with the front part of the latter over-
lapping the back part of the former (Fig. 5). Viewed from the
ventral surface, the anterior division has the appearance of a
spearhead with a short section of the shaft attached. From a
transverse line through the center of ossification the shaft extends
backward in a horizontal plane and lies ventral to, and gradually
merges with, the posterior division. Anterior to the center of
ossification the bone widens somewhat abruptly, then narrows
more gradually to form the point of the spear that is united with
the "prevomers." This surface is gently concave upward, and
along its median part two ridges starting at the center of ossifica-
tion gradually rise anteriorly, enclosing a groove between them.

The anterior part of the posterior division of the body of the
parasphenoid lies dorsal to the shaft of the anterior division. Its
front end begins a little ahead of a transverse plane through the
center of ossification. It is strongly concave upward in this
region, so that its lateral edges are directed almost dorsally.
Posteriorly the bone broadens, and the lateral curvature grows
less pronounced (Pl. IV, Fig. 1, PSPH). About 1.5 cm. behind
the center of ossification its ventral surface becomes confluent
with the ventral surface of the anterior division. A shallow groove
begins a little behind the center of ossification and widens rapidly
posteriorly. This ventral sulcus is probably incised posteriorly
by the aortic notch.

Somewhat behind a transverse plane through the center of
ossification the dorsolateral edges of the posterior division send
out ascending rami in the form of strong pointed splints directed
laterally, dorsally, and a little posteriorly (Fig. 5, ARP; also
Fig. 1 and Pl. III, Fig. 1). A side view of the parasphenoid shows
a deep lateral groove between the anterior end of the posterior
division of the body and the shaft of the anterior division. The
anterolateral edge of each ascending ramus is strengthened by a
ridge, whereas its posteromedial edge is thinned.

Anterior to the ascending ramus the dorsolateral edge of the
posterior division of the body is shallowly notched (Fig. 5, FIC).

The notch lies in a position to form the ventromedial boundary of the foramen for the internal carotid artery. Another notch that lies at the juncture of the posterior edge of the ascending ramus and the dorsolateral edge of the posterior division is interpreted as forming the inner edge of the foramen for the external carotid artery (Fig. 5, FEC). The carotid arteries lie close to these positions in Recent polyodontids and in *Saurichthys* (Stensiö, 1925, 1932). No other indications of foramina are discernible in the parasphenoid of *Paleopsephurus*.

The anterior division of the parasphenoid in *Polyodon* (Fig. 4) has a comparatively slight lateral expansion ahead of the center of ossification, then a marked constriction and another lateral expansion where it joins with the posterior ends of the "prevomers." Anterior to the constriction the bone is flat; posteriorly it is convex upward in contrast to the form in *Paleopsephurus*. The posterior end of the anterior division terminates abruptly in *Polyodon* in a ragged edge in line with the posterior edge of the ascending rami. The posterior division of the parasphenoid does not extend anteriorly beyond the front edge of the ascending rami. The posterior central groove on the ventral surface of the parasphenoid is present in *Polyodon*, but is narrower and deeper than in *Paleopsephurus*.

In a specimen of *Psephurus* 36 cm. long the shape of the parasphenoid is notably different from that in *Polyodon* or *Paleopsephurus*. The anterior division resembles that of the latter in its down-arching and its median ridges and groove, but is much narrower. The posterior division is strongly concave upward throughout its length and bears no median ventral sulcus. The posterior border of each ascending ramus extends laterally, dorsally, and anteriorly instead of posteriorly, as in *Paleopsephurus*. Furthermore, it is this edge that is thickened by a ridge and the front edge that is thinned. Another anterior extension of the parasphenoid is separated from the anterior edge of the ascending ramus and from the lateral edge of the main body of the bone by sharp notches (Fig. 6). This process extends mainly anteriorly and dorsally and somewhat laterally. The ventrally concave surfaces of the main ramus, the anterior process, and the lateral

part of the main body of the parasphenoid are so placed as to
lie in the plane of a segment of a broad cone whose apex is at the
point of union of the posterior edge of the ascending ramus and
the main body of the bone. This area is the site of the origin of
part of the ventromedial portion of the m. protractor hyomandi-
bularis. That division of the muscle in *Polyodon* is concealed
from ventral view by the parasphenoid bone and the overlying
cartilage (Danforth, 1913). The foramen for the internal carotid
artery of *Psephurus* lies in the cartilage exposed by the notch
between the ascending ramus and the anterior process.

The apparent presence of two ascending processes of the para-
sphenoid in *Psephurus* is of some interest in view of Stensiö's
comments regarding the parasphenoid of other fishes. He says
(1925, p. 86): "Thus we find in the Palaeoniscids the three fol-
lowing types, with regard to the processus ascendens: (1) A type
possessing a very large and broad processus ascendens on each
side of the corpus parasphenoidei, a processus ascendens which,
as far as is known up to now, seems to comprise the homologues
both to the processus ascendens in *Saurichthys* and sturgeons and
to the processus ascendens in *Amia, Lepidosteus,* Teleosts and
other Actinopterygians. (2) A type which has on each side of the
corpus parasphenoidei two well separated processes ascendentes,
an anterior smaller one homologous with that of *Amia, Lepidosteus,*
Teleosts and higher Actinopterygians, and a posterior large one
that seems to be homologous with that of sturgeons and *Saurich-
thys.* (3) Finally, a type in which the homologue of the posterior
larger process in the preceding type is more or less completely
reduced (*Birgeria*), so that with regard to the processus as-
cendens the parasphenoid approaches more or less that of *Amia,
Lepidosteus,* and other higher Actinopterygians."

As mentioned before, the specimen of *Psephurus* that was
examined is very young. It may be that the more medial notch
is due to incomplete development of the bone and that an adult
fish would show this to be part of an expansion of the main body
of the bone anterior to the center of ossification, similar to the
condition in *Paleopsephurus.* Its position dorsal to the plane of
what is here considered the anterior division of the body of the

parasphenoid suggests that *Psephurus* may have an anterior processus ascendens such as is described by Stensiö, even though it has lost articulation with the anterior pterygoidal region of the upper jaw.   The term "ascending ramus" is used instead of "processus ascendens" because the latter name is applied to a dorsal process of the palatoquadrate (Goodrich, 1930, p. 425). The relations of the opisthotic and the ventral plate of the ventral process of the lateral extrascapular to the parasphenoid in *Paleopsephurus* have already been discussed (pp. 172, 181).

Jaw Apparatus and Branchial Arches

The general composition of the mouth and its related bones in *Paleopsephurus* closely resembles the homologous structures in the modern *Psephurus*.   The fossil fish, however, contains several ossifications not found in the modern form.

The jaw apparatus had no bony connection with the cranium. It was probably attached to the hyomandibular by means of the unossified symplectic cartilage and the quadratosymplectic and quadratohyomandibular ligaments much as in the modern polyodontids (Tatarko, 1937, fig. 6, lghm).

The medial surface of the palatoquadrate cartilage was plated with a heavy dermal bone (Figs. 7–8, PT; Pl. II).   This bone may have been made up of several components, but since no traces of sutures or other indications of a compound origin were found, it is called the pterygoid.   It exists in *Polyodon* and *Psephurus* as a much lighter, narrower splint.

The posterior half of the pterygoid faces laterally and a little ventrally.   Its anterior half turns medially, so that it faces anterolaterally and somewhat more ventrally.   The center of ossification lies slightly anterior to this turn, and from it extend fine radiating plicae on the surface of the bone.   The central part of the dorsal edge is marked by a slight lateral ridge which, if it is comparable to that in *Polyodon*, indicates the dorsal extent of the palatoquadrate cartilage.   Both anteriorly and posteriorly the pterygoid extends less far than the maxillary.   The pterygoids appear to have met anteriorly in a symphasis.

On the ventral edge of the pterygoid, about midway between

its extremities, there is a well-marked notch of unknown function (Fig. 7; Pl. II).

Slightly overlapping the outside of the anteroventral edge of the pterygoid there is a thin plate of bone, represented in the matrix by the characteristic brown stain and bony granules, in much the same state of preservation as the opisthotic. This plate (Figs. 7–8, PAL 1) is about a centimeter wide and curves out-
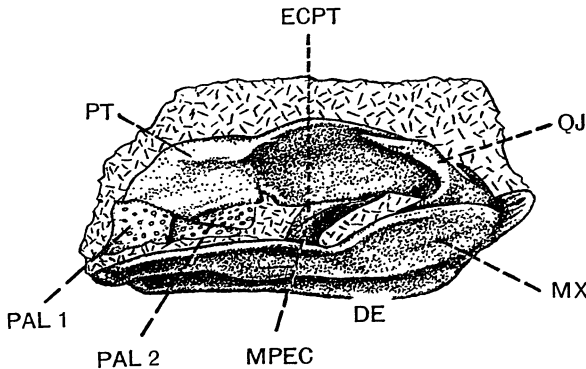
Fig. 7. *Paleopsephurus wilsoni*, No. 22206 U.M. Jaw apparatus from a lateral view. × 1

Abbreviations: DE, dentary; ECPT, ectopterygoid; MPEC, ectopterygoid process of the maxillary; MX, maxillary; PAL 1, palatine 1; PAL 2, palatine 2; PT, pterygoid; QJ, quadratojugal. × 1

ward and downward nearly to the outer edge of the anterior part of the maxillary. It is referred to here as palatine 1; it may easily be homologous to the autopalatine of palaeoniscids. A very thin similarly placed plate is described in *Polyodon* by Bridge (1878) as the mesopterygoid. Posterior and a little dorsomedial to palatine 1 of *Paleopsephurus* are one or two more plates, somewhat smaller than palatine 1, but otherwise similar, which, because of their indistinct outline, are collectively designated as palatine 2 in Figures 7 and 8 (Watson, 1925).

A small stout triangular bone extends antero-latero-ventrally from the middle of the ventral edge of the posterior half of the

pterygoid, and is suturally united by its posteroventral edge to a
strong process extending from the central part of the medial
surface of the maxillary. Since these two taken together mark
the anterior boundary of the oblong foramen of the m. adductor
mandibularis, they are interpreted as the ectopterygoid and the
ectopterygoid process of the maxillary. Watson (1925) shows
the ectopterygoid as bounding the anterior end of the foramen
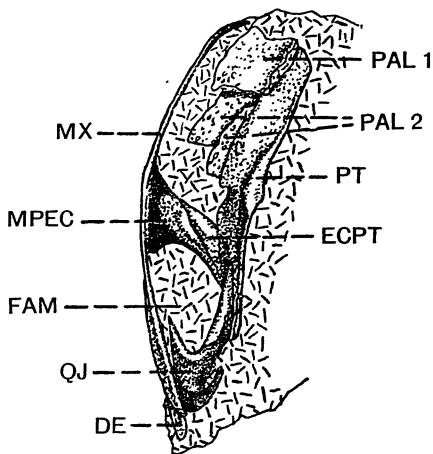
FIG. 8. *Paleopsephurus wilsoni*, No. 22206 U.M.
Jaw apparatus from a dorsal view. × 1

Abbreviations: FAM, oblong foramen from the
m. adductor mandibularis. Other lettering as
in Figure 7.

in the palaeoniscid *Elonichthys*, and Stensiö (1925) illustrates a
similar condition in *Saurichthys*.

The ectopterygoid process of the maxillary in *Paleopsephurus*
seems to be firmly united to it, for a careful examination revealed
no indication of a suture. The ectopterygoid does not appear to
be developed in other Polyodontidae or in the Acipenseridae. A
small process extending inwardly from the maxillary in a com-
parable position to the ectopterygoid process is clearly present
in the specimen of *Psephurus* that was examined.

The long, pointed ventral edge of the quadratojugal in *Paleo-*

psephurus (Figs. 7–9, QJ) lies slightly inside the extreme posterior portion of the dorsal edge of the maxillary bone. As it leaves the maxillary in an anterodorsal direction it narrows considerably, then turns somewhat more anteriorly and ends in an anteriorly directed point. This gives the front edge of the quadratojugal the shape of an open U. The dorsal part of the bone lies lateral to the face of the pterygoid near its posterodorsal edge.

On the posterodorsal edge of the quadratojugal a finger-like medial process (Fig. 9, QP) swings inward and follows a course parallel to the main body of the bone for half its length, so that a distinct cleft remains between these two parts.

No ossified quadratojugal exists in *Polyodon;* the cartilaginous orbital process (Bridge, 1878) lies in the position such a bone would have occupied. *Psephurus*, however, has a quadratojugal of almost exactly the same character as the one in *Paleopsephurus*. So far as is known, this bone has not been previously described. Tatarko (1937), who discussed the jaw apparatus of *Polyodon* and *Psephurus*, apparently overlooked the quadratojugal of *Psephurus*, although he had previously noted the presence of this bone in *Acipenser* (Tatarko, 1936). In *Psephurus* the medial process of the quadratojugal is present, as it is in *Paleopsephurus*. A careful examination of the structure in this region in *Psephurus* disclosed no special function of either the medial process or the notch between it and the main body of the bone. Possibly it serves to strengthen that area of the cartilaginous quadrate from which arise the symplectic and hyomandibular ligaments.

The rhipidistians had a quadratojugal that was united posteriorly with the preopercular, which carried the preoperculo-mandibular laterosensory canal. Stensiö (1925, p. 103), who describes a quadratojugal in *Saurichthys*, comments thus on the
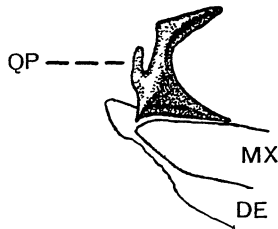

FIG. 9. *Paleopsephurus wilsoni,* No. 22206 U.M. Quadratojugal from a posterior oblique view. × 1

Abbreviations: DE, dentary; MX, maxillary; QP, quadrate process of the quadratojugal

condition of this bone in other chondrosteans: "About the same position and the same relations as the quadratojugal in *Saurichthys ornatus* is held by the bone in sturgeons interpreted by Parker 1882 (p. 172) and Iwanzow 1887 (p. 21) as the preoperculum and by Parker 1873 (p. 256), van Wijhe 1882 (p. 223), Traquair 1887 (p. 253), Woodward 1889 (p. 26), Woodward 1895 (p. 26) and Goodrich 1909 (fig. 293) and others as the jugal (supramaxillary); and this is also the case with the so-called jugal in *Chondrosteus* (Traquair 1887, p. 253; Woodward 1889, figs. 11, 12; 1895, figs. 2, 3; 1898, figs. 67, 68; Goodrich 1909, fig. 295, etc.). As the preopercular sensory canal in *Acipenser* has now been found to run in a vertical row of small bone-plates lying loose in the skin behind the so-called jugal or preoperculum (cf. Allis 1905, p. 484), everything thus indicates that the latter bone, i.e. the so-called jugal, must be the quadratojugal."

Westoll (1937a), who examined Stensiö's type material at Upsala, believes that the quadratojugal of the saurichthyids extends far enough posteriorly to be pierced by the preoperculo-mandibular sensory canal and therefore should be regarded as preopercular 2. He states also (p. 378) that "In *Cheirolepis* there is a possible remnant of the quadratojugal, not found in later members of the group if we except the very doubtful scale-bones (probably neomorphs) in *Polyopterus*." However, after being shown a number of palaeoniscids described by Nielsen (1936) he added the following postscript to his paper: "These show, in many cases, a small bone in the position of the quadrato-jugal of *Cheirolepis*, and Dr. Nielsen believes that the bone is associated with the vertical pit-line. This discovery does not affect the general conclusions advanced in this paper, merely showing that the bone in question is retained in the 'Palaeoniscids' longer than was known. It is possible, however, that it may affect the nomenclature of the cheek-bones in *Saurichthys*, where the course of the preopercular canal is not fully known."

If Westoll's conclusion regarding the quadratojugal be accepted, it leaves still in question the homology of the bone in *Psephurus* and *Paleopsephurus*. From all appearances it cannot be the preopercular because the preoperculomandibular canal lies

posterior to it in *Psephurus;* it cannot be the jugal because the closely related *Chondrosteus* has an obvious homologue of the bone called quadratojugal in *Paleopsephurus,* as well as a separate jugal much anterior to it (Watson, 1925); it cannot be the quadrate bone because (1) it is of dermal origin, (2) it forms no part of the articulation of the lower jaw, and (3) it lies lateral and dorsal to the m. adductor mandibularis. By elimination of other possibilities it seems that the bone cannot be anything other than the quadratojugal and the homologue of the quadrato-jugal of the crossopterygians and the Palaeoniscidae.

In *Paleopsephurus* the maxillary bone (Figs. 7–8, MX) seems to be composed of a single unit, as it is in other adult Polyodon-tidae. Its slightly expanded posterior third faces laterally and somewhat ventrally. Its anterior two thirds swings inward in an arc to meet the opposing maxillary anteriorly, and at the same point this portion twists in such a way that its outer surface faces much more ventrally than does the posterior third. Investigators who have studied the embryological conditions in the acipensers generally believe the maxillary of living paddlefish to be made up of several fused components (Stensiö, 1925; Sewertzoff, 1928; de Beer, 1937). Unfortunately, such an opinion cannot be either con-firmed or denied by the evidence in this specimen of *Paleopsephurus.*

The dentary (Fig. 7, DE) also appears to be a single bone. It has the same length as the maxillary and follows the same general curvature, but it is somewhat more posterior, as it is in *Psephurus.* Both the maxillary and the dentary of *Paleopse-phurus* are more robust than they are in modern polyodontids; in this respect they resemble *Crossopholis.* The dorsolateral sur-face of the Meckelian cartilage was plated with a bone whose homologue in *Polyodon* has formerly been referred to as the splenial (Traquair, 1877; Bridge, 1878). Recent investigators hold that the true splenial is not developed as a separate bone in the actinopterygians, with the possible exception of *Cheirolepis.* In *Saurichthys* the bone that corresponds most closely to the so-called splenial of the polyodontids is called the "mixicoronoid" by Stensiö (1925). In the palaeoniscids the prearticular (Watson, 1925) appears to be the homologue of the so-called splenial, and

because that term seems more indicative of its topographic position in *Paleopsephurus* than does "mixicoronoid," it is adopted here. Since the bone could not be freed from all matrix, its entire length is not known. A cross section is plainly shown in the diagonal break (Pl. IV, Fig. 1, PRA).

Some idea of the relation that the mouth apparatus bears to the rest of the head may be gained from Figure 1 and Plates I and II. The symphasis of the maxillaries lies on a transverse plane that passes approximately through the orbits. The posterior ends of the dentaries lie on a similar plane that passes through the center of ossification of the supratemporal bone. When the mouth was closed it resembled that of most sharks; when it was open it must have looked like that of *Psephurus*, which is large and protrusive and has an extensive gape.

The hyomandibular (Fig. 1; Pl. IV, Fig. 1, HYM) is a strong rod resembling that of *Psephurus* more than that of *Polyodon*. In *Paleopsephurus* it lies in nearly the same horizontal plane as the skull when the mouth is closed, so that its morphologically anterior surface faces ventrally and its morphologically posterior surface faces dorsally. It is horizontally widened at the head and vertically widened at the base. Its central part is well ossified, but the extremities are hollowed for the reception of the cartilaginous ends. The cartilaginous head of the hyomandibular in *Polyodon* and *Psephurus* articulates in a chondrocranial fossa just posterior to the ascending ramus of the parasphenoid, and since the hyomandibular in *Paleopsephurus* lies in much the same topographic position as it does in the Recent paddlefish, it can be assumed that it was articulated in a similar fashion and that it has been little disturbed. The relation of the hyomandibular to the opisthotic is described on page 172.

The dorsal (morphologically posterior) edge is straight as far as the posterior part of the bone, where it curves upward slightly. Its ventral edge is straight along its front half and curved sharply downward along its posterior half. This edge is formed by a strong ridge which, from a ventral view, makes up the entire width of the bone at its posterior end, arches slightly outward as it continues forward, then expands laterally and medially,

and forms the entire width of the bone at its anterior end. The space lying within the inner curve of this ridge is occupied by a strong shelf with a straight medial margin. Thus on the ventral surface of the hyomandibular there is a well-marked area for the insertion of the m. protractor hyomandibularis. The relations of this muscle will be discussed later (p. 225).

There is no visible trace of a symplectic or of an interhyal. The ceratohyal (Fig. 1; Pl. III, Fig. 2; Pl. IV, Fig. 1, CHY) of each side is well ossified throughout most of its length, but weakly at its ends. It is rod-shaped, flattened, and broadened at its extremities. The flattened surface of the anterior end faces ventro-medially, and that of the posterior end faces ventrolaterally.

Just anterior to the ceratohyals are the flat subtriangular hypo-hyals (Pl. III, Fig. 2, HHY), whose medial edges lie close to one another. These structures are not ossified in the Recent polyo-dontids, but were shown to be so in *Chondrosteus*, in which they have much the same shape and position as in *Paleopsephurus* (Jaekel, 1929).

Fortunately the ossifications of the branchial arches are preserved. Their exact lengths and positions could not be de-termined without the destruction of important overlying bones. A general idea of their extent could be gained, however, from the portions exposed along several fractures in the specimen.

The branchial arches were supported by flattened rods of cartilage covered by a thin layer of perichondral bone. A frac-ture that occurred parallel to the body of the parasphenoid reveals parts of the dorsal units of several arches. From what can be seen it is evident that the pharyngobranchial of at least the first gill arch and possibly that of the second had a bony sheath. The true extent of the epibranchial and ceratobranchials could not be determined. They are visible in a small area overlying the left cleithrum. This exposure shows that the sharp angle between the epibranchials and the ceratobranchials extends as far pos-teriorly as the anterior edge of the subopercular. Cross sections of the bony part of the branchial supports are plainly visible in the diagonal fracture and can be seen on Plate IV, Figure 1, BA. No trace of the gillrakers, gill bars, or basibranchials could be found.

Opercular Bones

It was hoped that some evidence of an opercular bone, such as occurs in *Chondrosteus*, could be found in *Paleopsephurus*, since its occurrence would indicate that the large bone in the opercular apparatus of the polyodontids is the true subopercular (Fig. 1, SOP; Pl. II), but, unfortunately, none seems to have been present. That the opercular has been lost in the acipensers and the subopercular retained is shown by the condition in *Chondrosteus*, in which the opercular is relatively small and the subopercular large. An evolutionary trend toward the same condition is also demonstrable among some of the palaeoniscids, an unknown member of which is believed by several authors to have been the ancestor of the acipenserids (Traquair, 1887; Woodward, 1889, 1898; Watson, 1925, 1928; Goodrich, 1930).

The subopercular (Fig. 1, SOP; Pl. II) in *Paleopsephurus* resembles that in *Psephurus* more than the one in *Polyodon*, and is considerably stouter than that of either of the living forms. The anterior margin is straight and vertical, with a strong attenuated projection extending forward from its dorsal third. The projection lies over the posterior half of the hyomandibular and was probably attached to it by connective tissue only, as in the Recent polyodontids. The posterior edge of the subopercular is convex backward and is deeply emarginated between strong rays extending out from the center of ossification. The center of ossification lies a little posterodorsal from the angle between the anterior margin and the ventral edge of the forward projection, and from it a strong lateral ridge extends outward close to the margin of each of these. The dorsal margin of the subopercular is fairly horizontal and lies a little above that of the anterior process.

A series of three or four small closely overlapped bones that are here considered to be the branchiostegal rays (Fig. 1, BSR) reach from the posterior tip of the ceratohyal to the medial surface of the ventral end of the subopercular. These bones do not present a clear-cut outline, and there is no certainty that they have been preserved in exactly their true position. Both *Polyodon* and

Psephurus have a single ventral bone with posterior rays whose anterior end is attached by connective tissue to the interhyal. It extends toward, but does not reach, the much-reduced subopercular. Authors who refer to this smaller ventral bone as the subopercular regard the larger dorsal one as the opercular (Goodrich, 1930; Holly, 1936).

Pectoral Girdle and Fins

The girdle as a whole is remarkable for its strong development as compared with that of the modern paddlefish. The supracleithrum (Fig. 10, SCL; Pl. II) is the most rugged bone in
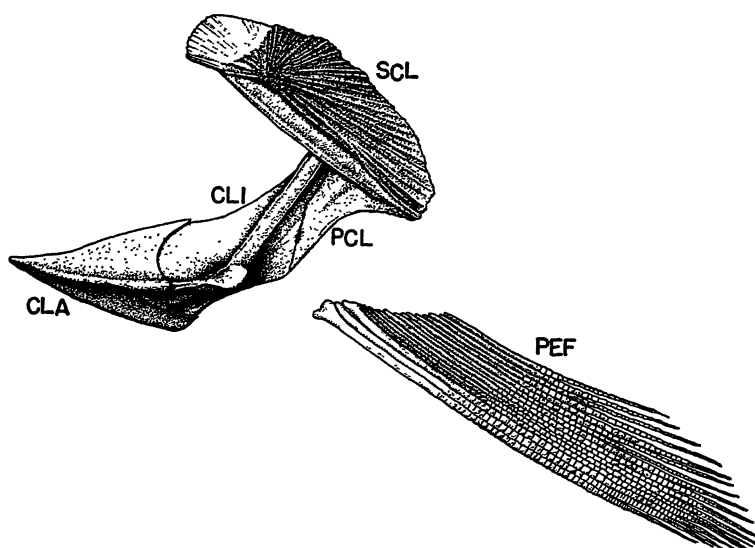
FIG. 10. *Paleopsephurus wilsoni*, No. 22206 U.M. Restoration of the pectoral girdle and fin. Some of the medial fin rays are enclosed in matrix, so that the exact number could not be determined. × ⅔

Abbreviations: CLA, clavicle; CLI, cleithrum; PCL, postcleithrum; PEF, pectoral fin; SCL, supracleithrum

Paleopsephurus. It is roughly oval, but with its anteroventral margin less curved than its posterodorsal margin. Its length, directed posteroventrally, is three times its greatest width. The center of ossification lies a third of the distance from its front end

and rather close to its lower margin. From this nodose center strong rather rough ridges and smaller rays extend outward over the surface in all directions except toward the anteroventral edge. This edge is in the form of a long narrow plate extending out somewhat laterally from the rest of the bone. The ridges extending anteriorly end in an abrupt line, so that the anterior fifth of the outer surface of the supracleithrum is comparatively smooth. This is probably the area that articulated with the medial surface of the lateral extrascapular and the suprascapular.

The powerful cleithrum (Fig. 10, CLI; Pl. II) resembles the cleithrum in the acipensers more markedly than that in the polyodons. Its posterodorsal edge is closely united by a suture to the anterior edge of the postcleithrum (Fig. 10, PCL), and the two bones together fit closely to the posterior two fifths of the medial surface of the supracleithrum. In the introduction to this paper it was mentioned that part of the shoulder girdle of a second specimen of *Paleopsephurus* was found. The portion showing the contact of the supracleithrum, cleithrum, and postcleithrum is practically all that was preserved in this specimen, but it gives a clear view of the medial surface and makes it plain that the postcleithrum and the cleithrum extend to the posterodorsal edge of the supracleithrum.

A strong laterally projecting prominence with a small oval face, slightly concave outward (Fig. 10), lies near the posteroventral edge of the cleithrum. From this lateral prominence a ridge extends posterodorsally, gradually diminishes in height, and disappears under the anteroventral margin of the supracleithrum. Extending forward from the lateral prominence of the cleithrum is a ridge that is continued on the clavicle as a lateral horizontal ridge and ends in a pointed anterior tip. The inner surface of the expanded posterior part of the clavicle is in close contact with the outer surface of the anterior part of the cleithrum. Their confluent surfaces lie dorsal to the lateral prominence, and the ridges curve sharply inward and upward, which gives the two bones taken together the appearance of a plowshare. This area forms the inner boundary for part of the branchial chamber.

The postcleithrum (Fig. 10, PCL) is united along its antero-

dorsal edge to the cleithrum, as described above. Ventrally the postcleithrum tapers off to a point at its distal end. As viewed from the side, its posteroventral margin is strongly concave. The same curvature is present, though less marked, on the postero-ventral margin of the cleithrum. In the living animal the space between this somewhat sinous posteroventral edge of the shoulder girdle and the pectoral fin must have been occupied by the unossi-fied scapulocoracoid cartilage.

From the horizontal lateral ridge of the clavicle (Fig. 10; Pl. III, Fig. 2; Pl. IV, Fig. 1, CLA) the ventral surface of the bone swings sharply medially and somewhat ventrally and slightly overlaps a similar flange from the opposing clavicle. Both the ventral and the dorsolateral surfaces of the bone narrow anteriorly to a point that lies well forward between the jaws.

Since the clavicles are relatively thin bones, they each have an inner counterpart of the lateral ridge in the form of a sulcus. Between the sulci of the two clavicles lies an azygous plate. The anterior portion and the ventral surface of this element could not be freed of matrix, but it is evident from what is exposed that it extended at least as far as the anterior ends of the clavicles and that it is as wide as the entire space between their sulci. An *Acipenser* that was examined has a similar scalelike bone lying in the same relative position, and Hennig (1925) shows in *Chon-drosteus hindenburgi* a V-shaped element, with its apex extending forward, that lies somewhat beyond the anterior ends of the clavicles. This he calls the "interclavicle," a name tentatively adopted here for the bone lying between the clavicles in *Paleo-psephurus*. The use of the term seems justified here, in spite of Romer's conviction (1924, p. 121) that "Paired cleithra and clavicles are also found in the more primitive bony fish, as Dipnoi, Crossopterygii and Chondrostei, although the interclavicle, which is probably developed as an expanded median ventral scale de-veloped in relation to the pectoral muscle is not found in fish."

The pectoral fin (Fig. 10, PEF; Pl. I, Fig. 1) is of much the same shape and construction as that of *Polyodon*. The presence in *Paleopsephurus* of a strong lateral prominence on the cleithrum upon which originated some of the lateral portion of the ventro-

lateral fin musculature (Romer, 1924) is presumptive evidence that the fin was held in a horizontal position in life (White, 1939) similar to the position of the fin in related modern fish. The fin rays are unsegmented for about the proximal quarter of their lengths and are strongly segmented for the remaining three quarters. Apparently no dichotomy of the rays is present, as there is in *Polyodon*. The exact number of fin rays could not be counted, since the medial rays were deeply buried by matrix. No pectoral radials were found.

Skeleton of the Caudal Region

A portion of the caudal region of another specimen of *Paleopsephurus wilsoni* was mentioned in the introduction to this paper. Some neural and hemal spines, some hypurals, the ventral caudal
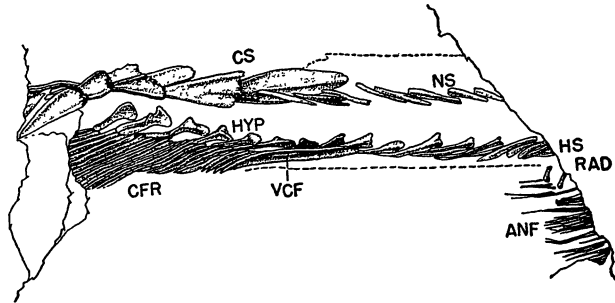
FIG. 11. *Paleopsephurus wilsoni*, No. 22207 U.M. Caudal region. $\times \frac{1}{2}$

Abbreviations: ANF, posterior tip of the anal fin; CFR, caudal fin rays; CS, caudal scutes; HS, hemal spines; HYP, hypurals; NS, neural spines; RAD, radials of the anal fin; VCF, ventral caudal fulcra

fulcra and some fin rays, the posterior tip of the anal fin, large flat oat-shaped scutes, and numerous minute denticles were preserved (Fig. 11). The blocks of rock probably containing the remainder of the anal and caudal fins and all the dorsal fulcra are missing. The following description is based on this specimen.

The last centimeter or two of the extreme tip of the anal fin (Fig. 11 ANF) remains as fine strips of articulated lepidotrichia.

Not enough of the fin is left to enable one to tell whether or not dichotomy had taken place. Two small bones, which are probably anal radials (Fig. 11, RAD), lie between the most dorsal fin rays and the body of the specimen.

A series of hemal spines is present (Fig. 11, HS). They are little more than thin splints dorsal to the tip of the anal fin. However, their bases become more expanded caudally, and in the region of the ventral fulcra and fin rays they have the characteristic appearance of chondrostean hypurals (Fig. 11, HYP).

The anterior ventral fulcrum is 3.8 cm. long and 0.5 cm. wide (Fig. 11, VCF). From a bluntly rounded anterior end it tapers to a point posteriorly. Its outer surface is comparatively smooth, being marked only by two very shallow grooves and a few lesser striae converging to the posterior tip. Four or five fulcra, about a third of the length of the first, follow in a tightly packed formation. It could not be determined whether or not their anterior edges were notched. Immediately behind and in serial continuation with these fulcra are strong tightly packed caudal fin rays. They were not preserved distally far enough to enable one to determine where segmentation began.

The neural spines (Fig. 11, NS), which are thin rods, are preserved posteriorly only as far as the first anterior oat-shaped scute.

This scute (Fig. 11, CS) is about 4 cm. long and 1 cm. wide. The inner surface is exposed, and it bears a low central ridge running the length of the scute. The similar scutes posterior to the first are badly broken and offer little to add to the description.

Between the proximal ends of the hemal and neural spines there is a smooth layer of brown-stained matrix, which is undoubtedly the fossil remains of the notochord. This organ is strongly persistent in all the known chondrosteans.

The minute denticles of *Paleopsephurus* will be described in the following section.

SQUAMATION OF THE POLYODONTIDAE

Although the bodies of *Polyodon* and *Psephurus* are generally described as naked, they do have "scales" of some interest in view of those present in *Paleopsephurus* and *Crossopholis*.

The *Polyodon* measuring 89.5 cm. that was examined has sixteen strong dorsal fulcra. The most anterior of these is 5.0 cm. long and 0.6 cm. wide at its widest part. It terminates anteriorly in a rounded end and tapers posteriorly to a sharp point. Externally it is almost identical in appearance with the anterior ventral caudal fulcrum of *Paleopsephurus*. From the center of the ventral surface of the anterior dorsal fulcrum in *Polyodon* two narrow rounded ridges extend anteriorly and enclose between them a narrow groove. The second fulcrum is only 3.7 cm. long, but it is 1.0 cm. wide at its anterior end. It has a low ventral ridge and a dorsal sulcus that terminate anteriorly in a notch 0.6 cm. long. The sixth fulcrum from the front is arrow-shaped and is 5.0 cm. long and 0.5 cm. wide at its anterior end. A broad straight-sided notch ends in a point 0.6 cm. from the anterior end of the fulcrum. A transverse section shows that the fulcrum is strongly concave ventrally to receive the convex dorsal surface of the next posterior. The fulcra behind the sixth are similar to it in shape, but gradually decrease in size.

In the *Psephurus* that was examined the most anterior fulcrum is 1.8 cm. long and 0.2 cm. wide. Externally it has the same appearance as the anterior fulcrum in *Polyodon*. Ventrally it is longitudinally concave to accommodate the next posterior fulcrum, which is shorter and wider but otherwise similar. The fourth fulcrum is longer and narrower than the first, and although it has a deep ventral sulcus there is no anterior notch. An adult *Psephurus* may show different conditions. In the specimens examined at the United States National Museum the number of fulcra ranged from six to ten. None of these specimens were over 89.0 cm. in total length.

In *Crossopholis* the dorsal fulcra are somewhat broken and are enclosed in matrix, so that their exact nature cannot be determined. Enough is evident (Pl. V) to show that they are extremely stout and end posteriorly in sharp points.

According to Woodward (1889, p. 30), *Pholidurus disjectus* is represented by "five more or less fragmentary fulcral scales, and portions of robust fin-rays, probably all found together, and belonging to the tail of one individual . . . . These scales are all

deeply overlapping, relatively broad, and notably flat; and the backwardly directed apex is rounded and obtuse. The small exposed portion is ornamented with thick ganoine in irregular dots and short wavy lines, more or less clustered, especially near the margin." He figures one of the fulcra in which the outline of the bifurcating inserted portion is restored from another specimen. In this figure the prominent anterior notch extends backward fully half the total length of the fulcrum. There is little apparent similarity between this fulcrum and any of those in *Psephurus*, to which, in Woodward's opinion, *Pholidurus* bears the closest resemblance among the living ganoids.

There appeared to be no trace of ganoine on the caudal scutes, fulcra, or head plates of *Paleopsephurus*, a lack which may be due to the altered condition of the bone. The ganoine has been entirely lost, however, from the scales and plates of the modern sturgeons and paddlefish, as well as from those of the fossil *Crossopholis*.

Concerning the caudal fin rays of *Pholidurus* Woodward (1889, p. 30) says that they are "also very robust, and the superficial ganoine is thick and rugose, not always completely covering the exposed faces of the successive joints." They appear from Woodward's figure to be much stouter and more widely separated from each other than those in *Paleopsephurus*, whose caudal fin rays are completely free from ornamentation and are so tightly packed as to seem to be somewhat flattened.

It is obvious from the descriptions given that *Pholidurus* and *Paleopsephurus* do not belong to the same genus. Furthermore, the differences between *Pholidurus* and the remaining known Polyodontidae are so marked that it evidently should be removed from the family.

Recent paddlefish have no ventral caudal fulcra. Those of *Paleopsephurus* have been described; those of *Crossopholis*, although badly broken, show that they are relatively stouter, shorter, and more curved, so that their distal ends are directed much more ventrally than they are in *Paleopsephurus*.

The caudal fins of all the known Polyodontidae are strongly heterocercal. The part of the body extending into the upper

lobe is covered laterally with small elongate rhomboidal scales
(Pl. V). The part of the tail that would show similar scales is
lacking in *Paleopsephurus*.

In 1904 Wagner noted the occurrence in Polyodon "of peculiar
small true scales over the surface lying over the entire scapular
arch and extending forward the entire length of the isthmus."
These denticles are so evident and so interesting that it is sur-
prising that they have not previously been described in more
detail. It seems necessary to describe them here for the sake of
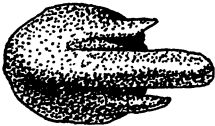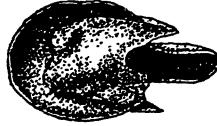comparison with the small denticles in *Crossopholis* and *Paleo-*
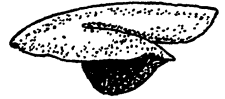

FIG. 12   FIG. 13   FIG. 14

FIGS. 12–14. *Polyodon spathula,* Outer, inner, and side views, respectively,
    of a denticle from the shoulder girdle region. × 20

psephurus. Figures 12, 13, and 14 show outer, inner, and side
views of one of these denticles taken from the *Polyodon* that is
89.5 cm. long. The Chinese paddlefish, *Psephurus*, has denticles
that are essentially the same in size, shape, and distribution.
They range in length from 0.1 to 0.2 cm.

Unfortunately, it was impossible at the time of examination
to make any histological investigation of the denticles. Under
the binocular microscope they appear to be composed of a thin
horny substance that is flexible when fresh and hard and brittle
when dry. The body of each denticle may be regarded as consisting
of an inner and an outer part. The outer part resembles a shallow
section from an ellipsoid, with its concave surface facing inwardly.
A finger-like projection or process extends posteriorly from the
center of the outer part of the denticle, and in the same plane, to
a distance well beyond the posterior margin. This projection is
hollow and bluntly rounded at its end. On either side are two
sharp spines, shorter and pointing in the same direction. The

inner part of the denticle is also a thin hollow plate, but with its concave surface facing outwardly. It is smaller than the outer part and fits inside it in such a way that its anterior edge lies in the hollow of and somewhat posterior to the anterior edge of the outer part. The two parts leave an aperture facing posteriorly over which the hollow finger-like posterior process extends. The inner part and the periphery of the outer part of the denticle are embedded in the skin; the remainder is exposed. These denticles are thickly placed over the region described by Wagner, but follow no regular pattern or arrangement.

In addition to the fulcra, the rhomboidal scales of the caudal lobe and the horny denticles of the shoulder girdle of *Polyodon*,
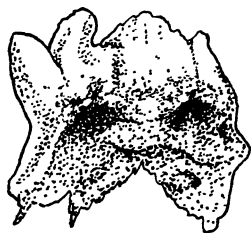

FIG. 15   FIG. 16

FIGS. 15–16. *Polyodon spathula*. Outer and inner
views, respectively, of a calcareous plate from
the trunk, near the shoulder girdle.   × 20

a fourth type of "scale," in the form of small calcareous plates, occurs over the entire trunk. Figure 15 shows an outer view and Figure 16 a side view of one of these plates taken from the trunk of a *Polyodon* slightly posterior to the shoulder girdle. Nothing similar is present in the *Psephurus* that was examined. Those of *Polyodon* are described by Collinge (1895) as follows: "Beneath the epidermis was a thin spongy layer of dermis, covering a series of small loosely arranged calcareous bodies, some of which lay in the underlying fibrous dermal layer. Amongst these, at varying distances, were isolated irregular plate-like calcareous bodies, resembling very closely those found in young *Lepido-stei* . . . . The formation of the scale never seems to get beyond

a stage common to the embryos of Ganoids and Teleosts." These calcareous platelike bodies, which are irregularly elliptical, are seldom longer than 0.2 cm., and they have their long axes generally at about right angles to the long axis of the animal. Nearly all have one to twelve or more small sharp outwardly directed tubercles, which often lie in a line on the long axis of the plate. In a typical area between the lateral line and the dorsal fin an average of thirty-six to the square centimeter was counted. None of these are in contact with another or lie in any fixed pattern or arrangement. Their presence makes the body of *Polyodon* feel decidedly rough.

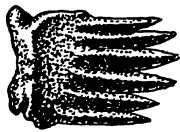A further peculiarity neither found in the other specimens of paddlefish that were examined nor described by previous authors is ex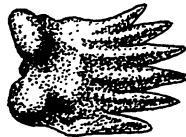hibited on the trunk of the *Polyodon* measuring 82 cm. long. The skin was marked, apparently by pigmentation, in such a way as to offer a scalelike pattern of small roughly rhomboidal light spots placed obliquely in rows. This is shown in the photograph (Pl. VI),

FIG. 17   FIG. 18

FIGS. 17–18. *Crossopholis magnicaudatus.* Outer and inner views of denticles from the trunk, near the dorsal fin. × 20

which also records a part of the lateral line with its branches and, less clearly, some of the calcareous bodies. The scalelike pattern bears no apparent relationship to the calcareous plates or to the underlying myocommata.

In his original description of *Crossopholis* Cope (1883) comments: "Scales numerous, in oblique series, not in contact; formed of a small grooved disk and several posterior spines." Later in the paper he says: "The scales are subquadrate in form and measure about a millimeter each way including the spines." Figure 17 shows the outside of one of these denticles and Figure 18, the inside of another. The number of posteriorly directed spines ranges from four to eight, with six the usual number. A well-marked inwardly projecting knob is present on each corner of the anterior edge of the inner surface. In the specimen of the *Crosso-*
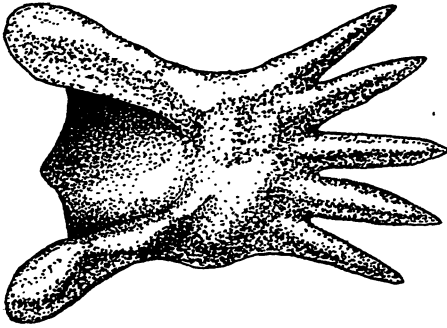
FIG. 19
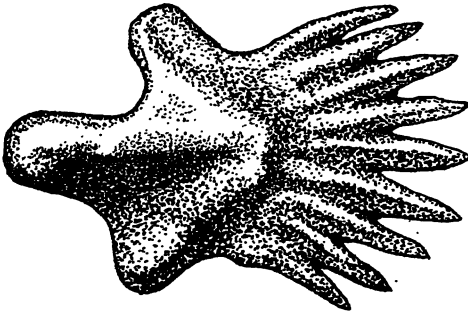
FIG. 20

FIGS. 19–20. *Paleopsephurus wilsoni.* Outer and inner views of denticles from the trunk, just posterior to the supracleithrum (Fig. 19) and near the anterior caudal scute (Fig. 20). × 20

pholis head only a single denticle was found, but it is unmistakably the same type as that which occurs in the trunk.

The denticles of the type illustrated in Figures 19 and 20 were present in abundance on all three specimens of *Paleopsephurus*. None were found anterior to the subopercular bone, but they were numerous directly posterior to the supracleithrum. Figure 19 is a view of the outside of one selected from this area. The denticles were plentiful over the entire caudal region and were scattered posterodorsally to the separate shoulder girdle. Figure 20 shows the appearance of the inside of one from the caudal region. These

denticles were selected for sketching with the purpose of illustrating their maximum difference in structure.

The denticles are 0.2 to 0.25 cm. long and 0.1 to 0.15 cm. wide. Each consists of a main body with three finger-like projections anteriorly and a number of spines directed fanwise posteriorly. The two outside projections extend a little outward from the midline of the denticle and lie in the same plane as the body and the spines. The central anterior projection is directed some-what inwardly from the main body of the denticle and is an ex-tension of a cuplike depression between the other two anterior projections. The posterior spines vary in number from five to nine; those in the caudal region generally have more than those near the shoulder girdle. The relative lengths of the anterior projections also vary; in some denticles the central projection is longer than the outside two; in others it is shorter. The central anterior projection is generally the longer when the posterior spines are more numerous. There is no apparent regular arrange-ment of the denticles in an oblique pattern, although this lack of pattern is possibly due to post-mortem distortion of the body.

There remains to be considered one more type of "scale" which is present in *Crossopholis* and *Paleopsephurus* but is lacking in the other fish discussed in this paper. It is represented by the three caudal "scuta" mentioned in Cope's description (1886) of *Crossopholis* and by the large oat-shaped scutes of *Paleopsephurus*. The bodies of these scutes are mostly lacking in *Crossopholis*, but they have left clear internal molds. Cope described the scutes as lying on the median dorsal line, which is not true, since they lie on the dorsolateral surface of the body, near the median dorsal line, and must be duplicated on the other side. He also stated that they had a median groove, apparently mistaking the groove made in the matrix by a central ridge on each scute as the groove of the scute itself. These scutes are the homologues of those described for *Paleopsephurus*.

The entire body of the *Scaphirhynchus*-like form mentioned in the introduction to this paper is covered with overlapping scales notably similar in size and shape to the caudal scutes found in *Crossopholis* and *Paleopsephurus*.

Interpretation of the Squamation of the Polyodontidae

The following interpretation is offered with the knowledge that it may have to be somewhat altered when a microscopic examination of thin sections is made.

The fulcra are formed as Goodrich (1930, p. 104) states: "The heterocercal caudal fin of the Chondrostei is built on essentially the same plan as that of the Selachii, but the epichordal lobe is further reduced and the lepidotrichia generally remain only as a double series of pointed scales often fused to ∧-shaped fulcra." Watson (1925, p. 822) reported the discovery of "a small but perfectly definite epichordal lobe at the extreme tip of the tail" in a single specimen of *Palaeoniscus major* from the Kupferschiefer of Thuringia.

The large oat-shaped scutes of the known fossil polyodontids may be an inheritance from a more completely covered ancestor whose squamation possibly resembled that of the undescribed acipenserid found with *Paleopsephurus*. The rhomboidal scales bordering the upturned caudal lobe are a characteristic of nearly all chondrostean ganoids. Their possible line of development and the change in the individual have been treated by Watson (1925) and Westoll (1937b).

Dr. Carl Hubbs suggested in conversation that the small spinous denticles may be closely allied to the placoid denticles of the sharks and pointed to the strong resemblance between those of the fossil polyodontids and those of sharks belonging to such families as the Carcharhinidae (*Hypoprion, Carcharhinus*) and the Cestraciontidae (*Cestracion;* see Radcliffe, 1914). Another interpretation is that the denticles have a dermal origin similar to that of ganoine in other chondrosteans and holosteans. If so, they probably developed as units separate from any bony scales that may or may not have underlain them.

Whatever their origin, it seems evident that a progressive simplification is illustrated by the condition of these denticles in the Cretaceous *Paleopsephurus*, the Eocene *Crossopholis*, and the denticles bordering the shoulder girdle of the modern polyodontids. That some type of scale, now lost, may have been on the trunks

of the ancestors of *Polyodon* is perhaps indicated by the oblique pattern made by the pigmentation. Progressive simplification in the squamation is also shown by the reduction of the caudal scutes from at least five in *Paleopsephurus* and three in *Crosso-* *pholis* to none in the living paddlefish.

The calcareous plates in the trunk of *Polyodon* are apparently a comparatively recent development and secondary in nature. It is not surprising that none could be found on the trunk of *Psephurus*, which is generally more "primitive" in structure than *Polyodon*.

COMPARISONS OF *PALEOPSEPHURUS* WITH RELATED FISH AND
A DISCUSSION OF THE EVOLUTIONARY TRENDS SUGGESTED

Paleopsephurus and Crossopholis

Cranial roofing bones. — The ventral surface of the roof in *Crossopholis* (Fig. 21) is exposed to view. Most of the bones of the median portion and left side are lacking.

The suprascapular, the median extrascapular, and the supra- temporal bones were either destroyed or were never present. Much of the lateral extrascapular (Fig. 21) is missing. The preserved portion shows that the bone was fairly robust and had a strong rounded lateral edge, as it does in *Paleopsephurus*. The ventral process was not preserved. The pattern of the remaining rostrocranial roofing bones appears to be much the same as it is in other known polyodontids. The bones are much lighter in weight than they are in *Paleopsephurus*, and in this respect bear a closer resemblance to *Polyodon*. The frontal of *Crossopholis* has an anterolateral process in the same position that it has in *Paleopsephurus*. A separate nasal bone could not be made out in *Crossopholis*. OL_1 has the characteristic elongate Y-shape found in other polyodontids.

The ventral rostrocranial skeleton. — The only portions of this part that are preserved are a few of the subrostral splints, which are somewhat fractured and are not completely freed from the matrix.

There are numerous small stellate bones scattered throughout the length of the rostrum but none lateral to it. Their position indicates that the lateral development of the spatula, strongly

Fig. 21. *Crossopholis magnicaudatus*. American Museum of Natural History, No. 2524. × ½

Abbreviations: AFL, anterior division of the fenestra longitudinalis; DE, dentary; DP, dentigerous plates; ESC, extrascapular; FR, frontal; "HHY," "hypohyals"; HYM, hyomandibular; IT, intertemporal; MLS, main laterosensory canal; MX, maxillary; OLₗ, posterior outer lateral dorsorostral; PFL, posterior division of the fenestra longitudinalis; PT, pterygoid; SCL, supracleithrum; SPO, suprapostorbital

present in *Polyodon* and supported by a bony reticulation, either must have been largely missing in *Crossopholis* as in *Psephurus* or, if developed, was unsupported by a network of bone. No supporting stellate bones were found in *Paleopsephurus* and, to judge from the otherwise excellent state of preservation, none were developed.

The ossifications of the main laterosensory canal (Fig. 21, MLS) that lie posterior to the dorsal end of the supracleithrum have been previously described in this paper (p. 184). No other structures definitely belonging to the laterosensory canal were discovered. In *Paleopsephurus* nothing of a comparable nature could be found.

The jaw apparatus. — The pterygoids (Fig. 21, PT) of *Crossopholis* are partly covered by matrix and other bones. From what could be made out, they appeared to be intermediate in size between those of *Paleopsephurus* and *Polyodon*. No palatines, ectopterygoids, or quadratojugals were found in *Crossopholis*. The maxillaries (Fig. 21, MX) and the dentaries (Fig. 21, DE) are much more robust and shorter than those in *Polyodon* and in this respect resemble those of *Paleopsephurus* more closely. The most interesting structures in the *Crossopholis* head are the dentigerous plates, with which the mouth was well equipped. There are four distinct plates visible, and evidence of two others is present (Fig. 21, DP). They are from 1.0 to 3.0 cm. long and 0.5 cm. wide, elliptical, and strongly concave on the probable surface of attachment. Concerning them Cope (1886) says: "Several dentigerous laminae lie among the jaw bones, from which they have been separated. They are concave on the inferior side, so as to embrace the alveolar borders, probably of the premaxillary (maxillary) bones, as those of the dentaries are too acute . . . . The bases of the teeth are round and close together. They measure .066 mm." It seems likely that these plates could have occupied the lower jaw as well as the upper by being partly supported by the Meckelian cartilage.

No trace of teeth was found in *Paleopsephurus*. Both jaws of young *Polyodons*, however, have numerous teeth, which are generally said to be lost in the adult fish. This may not always

be true. For example, the teeth are still present in both the 82 and the 89.5 cm. specimens that were examined; and Zograff (1887) stated that a *Polyodon* may retain its teeth during its whole lifetime. The following discussion of the teeth of the upper jaw of *Polyodon* is given by Allis (1919): "The anterior portion of the ventral edge of the (maxillary) splint is furnished with small teeth, and, extending approximately the same distance along the dorsomesial edge of the palatoquadrate, there is a row of somewhat stronger teeth. The bone to which these latter are attached fits closely upon the related edge of the palatoquadrate, and although fused anteriorly with the pterygoid splint of Bridge's description, it has markedly the appearance of being of independent origin. It is called by Gegenbaur (1889, p. 342) the palatine, but it is to be noted that it is, even in my quite young specimens, definitely of membrane origin, and that it lies along the dorsomesial, instead of the ventrolateral, edge of the palatoquadrate cartilage." The separation of the dentigerous plates from the jaw bones in *Crossopholis* further confirms Allis' conclusion regarding their independent origin in *Polyodon*. The teeth are more strongly developed in the 36 cm. *Psephurus* than in a *Polyodon* of slightly larger size.

To judge from what is exposed of the hyomandibular in *Crossopholis* (Fig. 21, HYM) it appears to be very similar to the same bone in *Paleopsephurus*. In the fossil it is turned around from its natural position, and Cope thought that it might be convex anteriorly, but qualified the statement by saying that this apparent anomaly might be due to injury of the specimen. Lying between and somewhat ventral to the lower jaw bones is a pair of smaller bones that are robust, subquadrangular, and hollowed at their ends. Their position and size indicate that they must be hypohyals (Fig. 21, "HHY"), but they are peculiarly and strongly rugose on their concave (medial?) surfaces. If these are the hypohyals, they are heavier and of a different shape from those in *Paleopsephurus*.

The opercular bones are too poorly preserved, because of destruction of parts or burial in the matrix, to enable one to make satisfactory comparisons with those of other fish.

FIG. 22. *Polyodon spathula.* Left half with superficial tissue and fat removed; right half shows the approximate course of the laterosensory canal. Cartilage is indicated by stippled areas

Abbreviations: AFL, anterior division of the fenestra longitudinalis; EPF, epiphyseal structure; ESC, extrascapular; FR, frontal; ILS, postorbital division of the infraorbital laterosensory canal; IT, intertemporal; M.RHM, mm. retractor hyomandibularis et opercularis; OL_1, posterior outer lateral dorsorostral; PAR, parietal; PFL, posterior division of the fenestra longitudinalis; PMLS, preopercular-mandibular laterosensory canal; SLS, supraorbital laterosensory canal; SPO, suprapostorbital; STLS, supratemporal branch of the laterosensory canal. $\times \frac{2}{5}$
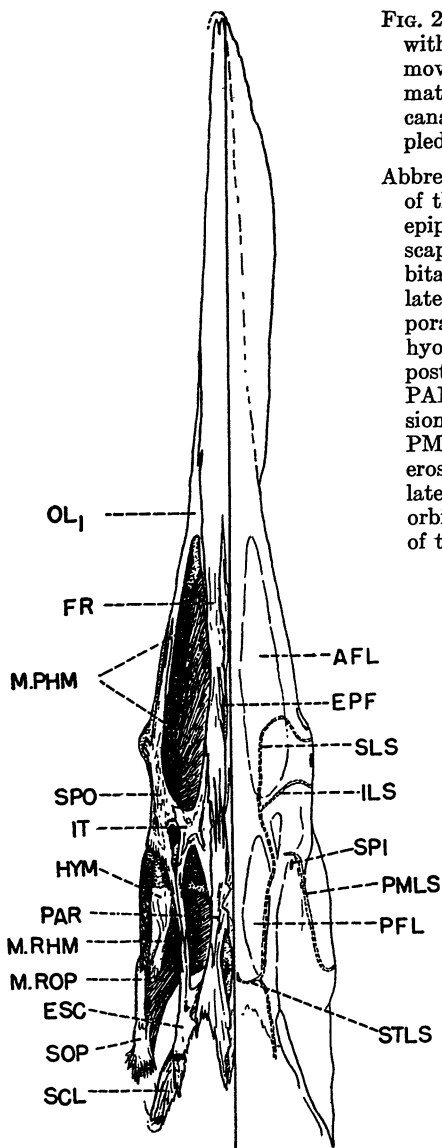
FIG. 23. *Psephurus gladius.* Left half with superficial tissue and fat removed; right half showing the apparent course of the laterosensory canals. Cartilage is indicated by stippled areas

Abbreviations: AFL, anterior division of the fenestra longitudinalis; EPF, epiphyseal fenestra; ESC, extrascapular; FR, frontal; HYM, hyomandibular; ILS, postorbital division of the infraorbital laterosensory canal; IT, intertemporal; M.PHM, m. protractor hyomandibularis; M.RHM, m. retractor hyomandibularis; M.ROP, m. retractor opercularis; OL₁, posterior outer lateral dorsorostral; PAR, parietal; PFL, posterior division of the fenestra longitudinalis; PMLS, preopercular-mandibular laterosensory canal; SCL, supracleithrum; SLS, supraorbital laterosensory canal; SOP, subopercular; SPI, dorsal opening of the spiracular canal; SPO, suprapostorbital; STLS, supratemporal branch of the laterosensory canal. × ⅗
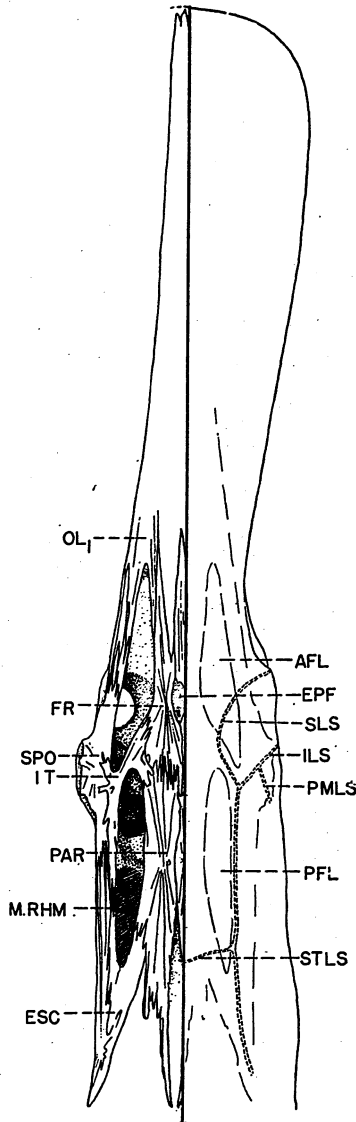
Parts of both supracleithra (epiclavicles of Cope's description) are preserved. Compared to those of *Paleopsephurus* they are longer, lighter in weight, and less sculptured, and the antero-ventral margin is incised in the shape of a widely obtuse angle instead of being rounded outwardly.

Except for the large caudal scutes, the tail region of *Crossopholis* bears a remarkable resemblance to that of *Chondrosteus*.

Paleopsephurus and the Modern Polyodontidae

It has been impossible adequately to interpret the conditions in *Paleopsephurus* without constantly referring to those in *Polyodon* and *Psephurus*. Many of the features of these two fish have had to be described separately. A tabular summary of material already covered is presented here. In the third column of the table below the condition described applies to both *Polyodon* and *Psephurus* unless otherwise stated.

TABLE I

COMPARISON OF THE STRUCTURE OF *PALEOPSEPHURUS*
AND RECENT POLYODONTIDAE

Structure	*Paleopsephurus*	Recent Polyodontidae
Chrondrocranium	Not preserved, but presumably massive	Massive
Opisthotic	A thin plate, probably pierced by the vagus nerve	A very thin plate, smaller and not pierced by the vagus nerve
Proötic	Possibly combined with the opisthotic	Separately present as a very small thin plate
"Epiotic"	A tentative name for a bone of uncertain origin	Lacking
Cranial roofing bones	Comparatively heavy, strongly united, ornamented	Lighter in weight, less ornamented, fewer
Nuchals	Three or four present	Lacking
Median extra-scapulars	Two present	Lacking
Parietals	Present, with a well-developed common keel at the median suture	Present, sometimes incompletely joined along the midline; median keel feebly developed

Structure	*Paleopsephurus*	Recent Polyodontidae
Frontals	Present	Present, but with the extension to the intertemporals less well developed and the process to the nasals lacking
Dorsorostrals ...	Present	Present and more numerous
Suprascapulars ..	Present	Lacking
Lateral extrascapulars	Present	Present, and with the ventral process more strongly developed
Supratemporals .	Present	Lacking
Nasals	Present, and with a process extending toward the frontals	Questionably present as a separate bone, no process toward frontals
Stellate supports for rostral flaps	Lacking	Strongly present in *Polyodon*, weakly so in *Psephurus*
Parasphenoid ...	Stoutly developed, with notches for internal and external carotid arteries	More lightly constructed, no foraminal notches; *Psephurus* possibly with anterior ascending ramus
Laterosensory canals	Untraceable, but probably similar to Recent forms	Present and often enclosed in small tubular ossicles
Visceral skeleton	Ossifications more numerous and more strongly developed than in Recent forms	More cartilaginous
Pterygoid	Robust	Lighter in weight, no notch on ventral edge
Palatines	Several present as thin plates	Anterior one present as a very thin small plate
Ectopterygoid ...	Present	Lacking
Quadratojugal ..	Present	Lacking in *Polyodon*, present in *Psephurus*
Maxillary	With medial process united suturally to the ectopterygoid	Lighter and relatively longer. Medial process slightly developed in *Psephurus*, and absent in *Polyodon*
Dentary	Present	Less robust
Hyomandibular .	Robust	Robust

TABLE I (*Concluded*)

Structure	*Paleopsephurus*	Recent Polyodontidae
Symplectic	Probably cartilaginous	Cartilaginous
Interhyal	Probably cartilaginous	Cartilaginous
Ceratohyal	Well ossified	Much less well ossified
Hypohyal	Ossified	Cartilaginous
Branchial arch supports	Mostly covered with a perichondral sheath	Cartilaginous, small ossifications on ceratobranchials and epibranchials only
Bones of the opercular fold	Subopercular and branchiostegal rays present	Same bones present, but the subopercular much reduced
Shoulder girdle and pectoral fin	Strongly developed; supracleithra, cleithra, postcleithra, clavicles, and interclavicle present	Same bones present, except interclavicle, but considerably reduced
Neural spines . . .	Ossified	Cartilaginous
Hemal spines and hypurals	Ossified	Cartilaginous
Squamation: Small denticles . .	Probably present over the entire trunk	Present over the shoulder girdle, but different in form
Calcareous plates	Lacking	Present on trunk region of *Polyodon*
Dorsal caudal fulcra	Present	Present
Ventral caudal fulcra	Present	Lacking
Dorsal caudal scutes	Present	Lacking
Small, rhomboidal caudal scales . .	Not known but probably present	Present

Jaw Musculature of the Polyodontidae

The jaw musculature in *Polyodon* has been adequately described by Danforth (1913) and Adams (1919) and briefly considered by Tatarko (1937). The differences between *Polyodon*

and *Psephurus*, particularly with respect to the m. protractor hyomandibularis, are important in an attempt to interpret the jaw action of *Paleopsephurus*.

Danforth (1913, p. 114), in speaking of the anterior division of the m. adductor mandibularis in *Polyodon*, says: "Anteriorly it is horizontal in position and occupies the space between the m. protractor hyomandibularis above and the palatoquadrate cartilage and maxillary below. Near the angle of the mouth it passes under a strong triangular fascia and turns abruptly downward to be inserted (*a*) in the anterior part of a shallow groove in Meckel's cartilage, and (*b*) on the median aspect of the overlying dentary bone." The muscle must have been similarly placed in *Paleopsephurus*, and the unusually strong brace between the maxillary and the pterygoid formed by the ectopterygoid and the medial maxillary process, together with the presence of a greater lateral distance between the maxillary and the pterygoid as compared with that in *Polyodon*, indicates that the m. adductor mandibularis was more strongly developed in *Paleopsephurus* than in *Polyodon*. The ectopterygoid–maxillary process lies in a position to receive the strain of the m. adductor mandibularis muscle where it turns ventrally to enter the lower jaw.

The m. protractor hyomandibularis of *Polyodon* has been described by Danforth (1913, p. 117) as "a large muscle, which in *Polyodon* arises in two separate parts, which soon unite. The smaller portion, whose fibers constitute the ventro-median part of the muscle, arises laterally on the cartilaginous base of the skull from a small area lying medial to the anterior opening of the facial canal, close to the roof of the mouth and immediately in front of the spiracular cleft. From below its origin is concealed by the parasphenoid bone and the overlying cartilage. The second and much larger portion of the muscle arises from the postorbital process, from the side of the chondrocranium and from the overhanging supraorbital cartilage, nearly as far forward as the olfactory capsule. The most anterior fibers, which are somewhat tendinous at their origin, are dorsal and medial to the eye. This muscle fills the angle between the hyomandibular and the skull and presses against the membrane stretching across the

spiracular canal in front. With the preceding muscle (m. adductor mandibularis) it fills out the side of the face. It is inserted on the anterior aspect of the hyomandibular, from the lateral margin of the spiracular canal throughout the middle third of the cartilage." In this description it is important to note that none of the dorsal portion of the muscle reaches farther anterior than the nasal capsule. In the *Polyodon* that was examined only a few muscular fibers extended a little forward both dorsally and ventrally to the optic stalk on the orbital wall (Fig. 22).

In *Psephurus* the condition in this region is quite different. The m. protractor hyomandibularis is much more powerful than it is in *Polyodon*. The belly of the muscle is larger at the head of the hyomandibular in the 36 cm. *Psephurus* than in the 82 cm. *Polyodon*. In *Psephurus* the largest part of this muscle originates strongly on the rostrocranial cartilage just ventral to the outer edge of the frontal, extending from nearly the anterior tip of the fenestra longitudinalis posterior to the notch of the intertemporal (Fig. 23, M.PHM). This origin extends anterior to the eye for a distance equal to the length of the hyomandibular. The posterior portion of the muscle originating from the rostrocranial cartilage is directed downward, outward, and then sharply backward and is inserted on the anteroventral surface of the hyomandibular. As the muscle makes this turn it swings around a cartilaginous rod with a conical base that extends dorsolaterally from the central part of the dorsal edge of the posterior orbital wall formed by the sphenotic process of the chondrocranium. This rod lies directly anterior to the chondrocranial canal of the spiracular diverticulum and extends to the ventral surface of the suprapostorbital near its medial edge and close to its center of ossification. A similar structure is present in the polyodons that were examined.

The medially directed styliform process of the suprapostorbital described in this paper in *Paleopsephurus* lies in a position corresponding to that of the rod described above in *Polyodon* and *Psephurus*. This suprapostorbital process probably either lay adjacent to a cartilaginous rod similar to that in the Recent paddlefish or was supplanted by such a rod later in the group's

history. The position of the suprapostorbital process in *Paleo-psephurus* would permit it to act as a brace on the line of turning of the posterior part of the m. protractor hyomandibularis originating on the rostrocranial cartilage, thus functioning in a manner similar to the homologous structure in *Psephurus*. There are several other indications that the m. protractor hyomandibularis was strongly developed in *Paleopsephurus:* (1) the deep lateral groove between the overlapping portions of the anterior division and posterior division of the parasphenoid (the description of the parasphenoid in *Psephurus*, p. 199, states that the comparable region serves as the area of origin for a part of the medioventral portion of the m. protractor hyomandibularis); (2) the down-arching of the subrostrocranial support in both *Psephurus* and *Paleopsephurus;* (3) the greater length of the combined anterior and middle divisions of the fenestra longitudinalis in these two forms than in *Polyodon;* (4) the strong shelf for the insertion of this muscle on the hyomandibular of *Paleopsephurus;* and (5) the more pronounced down-curving of the ventral edge of the distal end of the hyomandibular in *Paleopsephurus* and *Psephurus* than in *Polyodon.*

The function of the m. protractor hyomandibularis is to rotate the hyomandibular forward and a little outward on its proximal articulation (Danforth, 1913; Adams, 1919). The strong development of this muscle in *Psephurus* and the acipensers is needed to swing the protrusive mouth forward and downward. Although the gape of the mouth in *Polyodon* is comparatively larger than those in the two fish just mentioned, the mouth is not protrusive, the anterior end of the upper jaw arch being held firmly in place by connective tissue.

The conclusion drawn from the foregoing evidence is that the jaw apparatus of *Paleopsephurus* was strongly protrusive and that the anterior attachment of the upper jaw in *Polyodon* is secondary in character.

Occipital Musculature of the Polyodontidae

In *Polyodon* and *Psephurus* the ventral process of the lateral extrascapular is longer and wider than it is in *Paleopsephurus*,

and is somewhat larger in *Polyodon* than in *Psephurus*. In the
living forms the medial surface of the ventral process is occupied
by a part of the insertion of the lateral trunk muscle (Bridge,
1878; Danforth, 1913). This is a bulky muscle that anteriorly
fills the space between the ventral process and the axial skeleton.
Its large size and powerful insertion are undoubtedly associated
with the peculiar swimming habit of *Polyodon*, which in turn is
related to the method by which the fish feeds. The first accurate
description of its feeding habits was that by Stockard (1907);
later on they were treated by Norris (1923) and Thompson
(1934, p. 1). Thompson says, "The mouth is unusually large
and the gill arches are furnished with numerous long gill rakers
which strain out the food organisms as the fish swims about with
its mouth open. It swims unceasingly in a monotonous rhythm
and swings the rostrum from side to side in a wide arc. It has
been supposed that these movements of the rostrum are of use
in beating small animal life from the vegetation in weedy lakes,
but there is no evidence of any active digging." It is also probable
that the thousands of sensory pores or nerve pits scattered over
the rostrum are useful in detecting plankton, and the rostral
swinging would aid them in this function.

In the 36 cm. *Psephurus* (Kimura, 1934) the gillrakers are only
about a third of the length of those in a *Polyodon* of a slightly larger
size (Imms, 1904). They are much less numerous, more widely
spaced, flatter throughout their length, and rounded distally.

The evolutionary trend toward the *Polyodon* habit of feeding
and possibly away from some other habit, such as bottom grubbing
or ingestion of organisms larger than plankton, is indicated by
the following evidence: (1) the smaller ventral process of the
lateral extrascapular in *Paleopsephurus* for the origin of part of the
lateral trunk muscle; (2) the smaller size of the mouth in *Paleo-
psephurus;* (3) the apparently more powerful development of the
m. adductor mandibularis in *Paleopsephurus;* (4) the narrower
rostrum in *Psephurus* and probably in *Paleopsephurus* and *Crosso-
pholis* as compared to that in *Polyodon;* and (5) the more de-
generate condition of the teeth in *Polyodon* as compared with the
condition of the teeth in *Psephurus* and *Crossopholis.*

Relation of Rostral to Body Lengths in the Polyodontidae

The ratios of the length of the rostrum to the total length of the head in *Paleopsephurus* and *Crossopholis* and in the 89.5 cm. *Polyodon* are as follows:

	Tip of snout to anterior edge of postorbital process	*Tip of snout to posterolateral corner of lateral extrascapular*	*Ratio*
Paleopsephurus	17.5 cm.	25.5 cm.	0.68
Crossopholis	20.0 cm.	28.5 cm.	0.70
Polyodon	26.0 cm.	36.5 cm.	0.71

The slight differences that exist among these ratios are less than sometimes exist among those of various polyodons of the same total length (Stockard, 1907; Thompson, 1934). It is recognized by authors familiar with the paddlefish that the relative length of the rostrum decreases with the increase in total body length. Thompson (1934) states that the maximum relative length of the rostrum occurs in polyodons of about 25.0 cm. total length. Below that total length the relative rostral length decreases. In the smallest *Polyodon* known, one of 0.17 cm. (Thompson, 1933, 1934), the rostrum projects very little beyond the anterior extremity of the mouth. It seems likely that Cope (1886) was mistaken in supposing that the rostrum of *Crossopholis* was relatively shorter than it is in modern forms. Even in *Paleopsephurus*, which lived during Upper Cretaceous time, it is apparent that the rostrum was almost as long as that of a Recent paddlefish having a head of the same total length.

In attempting to arrive at some reasonable estimates for the total lengths of *Paleopsephurus* and *Crossopholis* it was necessary to consider the change in relative growth rates of the rostrum and the total body in *Polyodon*. The result of this study is a formula, based on Stockard's measurements and those of the specimens available here, that describes a curve showing with reasonable accuracy the rostrum to total length relationship in polyodons over 60 cm. long. It was later discovered that Thompson (1934) had accumulated numerous data on this subject, and had worked out a logarithmic curve illustrating the relationship

between the length of the rostrum and the length of the body not including the rostrum. . Since no formula accompanies his data and since his conclusions must have been based mainly on inspection of the curve, the formula mentioned above will be used here ($y = 2.8 + 0.21\ x$, where y equals the length of the rostrum as measured from the anterior edge of the eye and x equals the total length of the body). When the ratio in *Psephurus* was plotted on the curve described by the formula given above, it was found to fit on the line almost exactly. As computed by this formula, the total length of *Paleopsephurus* would be about 65 cm., and the total length of *Crossopholis* would be about 77 cm., rather than a meter, as estimated by Cope. These figures are, of course, only approximate and are based on the assumption that the bodies of the forms compared were in much the same proportions as in polyodons. This assumption, in view of the similarity of the rostrum to total head ratios noted above, does not seem unreasonable.

PLACE OF THE POLYODONTIDAE AMONG THE ACTINOPTERYGIANS

Since this paper is primarily a morphological study, the arguments concerning the systematic status of the Polyodontidae and the Acipenseridae will not be discussed here. The many similarities of these two groups (comprising the so-called acipenseroids) to the sharks, particularly in the structure of the soft parts, led Bridge (1878) and, later on, Sewertzoff (1923, 1926, 1928, and other papers) to regard the acipenseroids as descended directly from the selachians without the interposition of palaeoniscid-like forms. The majority of the authors who have dealt with this subject question Sewertzoff's thesis and believe that the acipenseroids descended from some unknown palaeoniscid-like fish.

This question is further discussed by Stensiö (1921, 1925, 1932), Traquair (1877), Woodward (1889, 1898), Regan (1904), Allis (1926), Bugeaw (1929), Watson (1925, 1928), Goodrich (1930), Brough (1931, 1936), and others whose papers will be found in the bibliographies of the works already listed. Brief reviews of the problem are given by Gregory (1933) and Säve-Söderbergh (1934).

SUMMARY AND CONCLUSIONS

The osteology of *Paleopsephurus wilsoni*, gen. nov., sp. nov., is described and figured in some detail. Many comparisons are drawn between structures in *Paleopsephurus* and those believed to be homologous in other fish.

Several morphological features of *Polyodon* and *Psephurus* are described in detail for the first time.

A macroscopic study is made of the squamation in the Polyodontidae, and the suggestion is offered that *Pholidurus disjectus* be removed from the family.

The jaw and occipital musculature of the Polyodontidae is discussed with the view of showing the character and habits of *Paleopsephurus*.

The ratios between the rostral lengths and the total body lengths in the Polyodontidae are discussed, and Cope's estimate of the length of *Crossopholis* is revised.

The conclusions drawn from these studies may be summarized as follows:

(1) The known members of the Polyodontidae form a closely allied group related to the Acipenseridae and more remotely related to the Palaeoniscidae.

(2) *Paleopsephurus* and *Crossopholis*, although showing some differences from the Recent paddlefish, cannot be far from their line of ancestry.

(3) *Psephurus* is less specialized than *Polyodon* and shows a little more similarity to the fossil members of the family.

(4) Recent paddlefish have evolved from a line of more highly ossified ancestors. Reduction of the bony structure has been general, but it is particularly noticeable in the roofing bones of the occipital region, the visceral skeleton, the shoulder girdle, and the squamation.

(5) In some particulars as, for example, the more numerous and better united plating bones of the roof and the stronger shoulder girdle, *Paleopsephurus* bears a stronger similarity to the Acipenseridae than do the Recent Polyodontidae.

(6) There is a quadratojugal in many acipenseroids homolo-

gous to the bone so called in the rhipidistians and the lower Palaeoniscidae.

(7) The mouth apparatus of *Paleopsephurus* was protrusive.

(8) In the Polyodontidae there is an indication of a change in the mouth parts that suggests a change in feeding habits culminating in an exclusive diet of free-swimming plankton.

(9) The length of the rostrum in comparison with the total length of the body as exhibited by modern Polyodontidae was attained in the family by Upper Cretaceous time.

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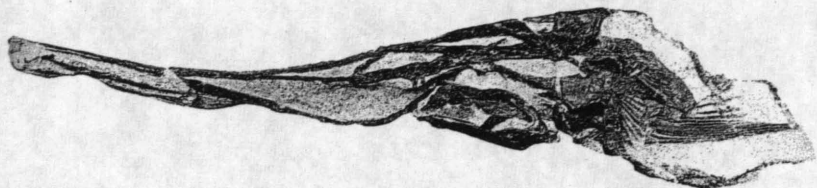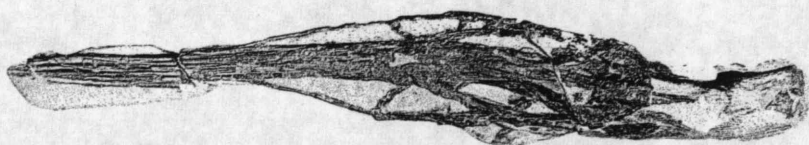
PLATE I

FIG. 1

FIG. 2

FIG. 1. *Paleopsephurus wilsoni*, No. 22206 U.M. Lateral view. $\times \frac{1}{3}$
FIG. 2. *Paleopsephurus wilsoni*, dorsal view. $\times \frac{1}{3}$

PLATE II

Paleopsephurus wilsoni, lateral view, showing particularly the opercular and jaw apparatus. × 1
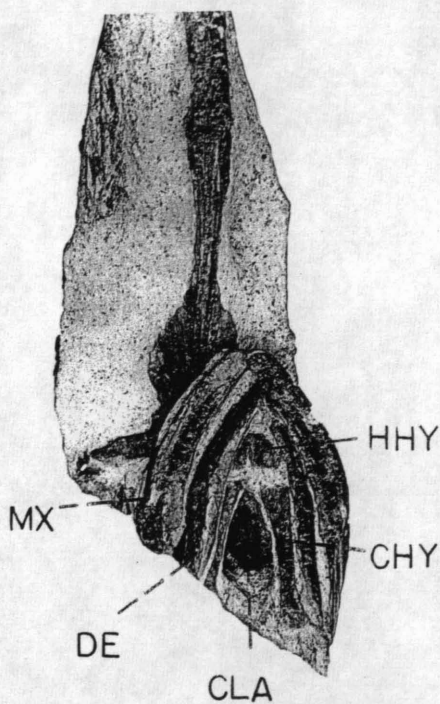
PLATE III

Fig. 1   Fig. 2

FIG. 1. *Paleopsephurus wilsoni*, No. 22206 U.M. Ventral view of the parasphenoid. × ⅔

FIG. 2. *Paleopsephurus wilsoni*, No. 22206 U.M. Ventral view of jaw and part of hyoid apparatus. × ⅔. Abbreviations: CHY, ceratohyal; CLA, clavicle; DE, dentary; HHY, hypohyal; MX, maxillary

EXPLANATION OF PLATE IV

Paleopsephurus wilsoni, 22206 U.M. × $\frac{3}{2}$

FIG. 1. Anterior oblique view of a diagonal fracture through the specime

FIG. 2. Posterior oblique view of the anterior dorsal portion of the
fracture

Abbreviations: BA, perichondral bony sheaths of the branchial ar
CHY, ceratohyal; CLA, clavicle; CLI, cleithrum; DVP, dorsal fl
of the ventral process of the lateral extrascapular; "EPI," anterod
tip of the "eipotic"; HYM, hyomandibular; OPIS, opisthotic; I
prearticular; PSPH, parasphenoid; PT, pterygoid; VF, vagus fora:
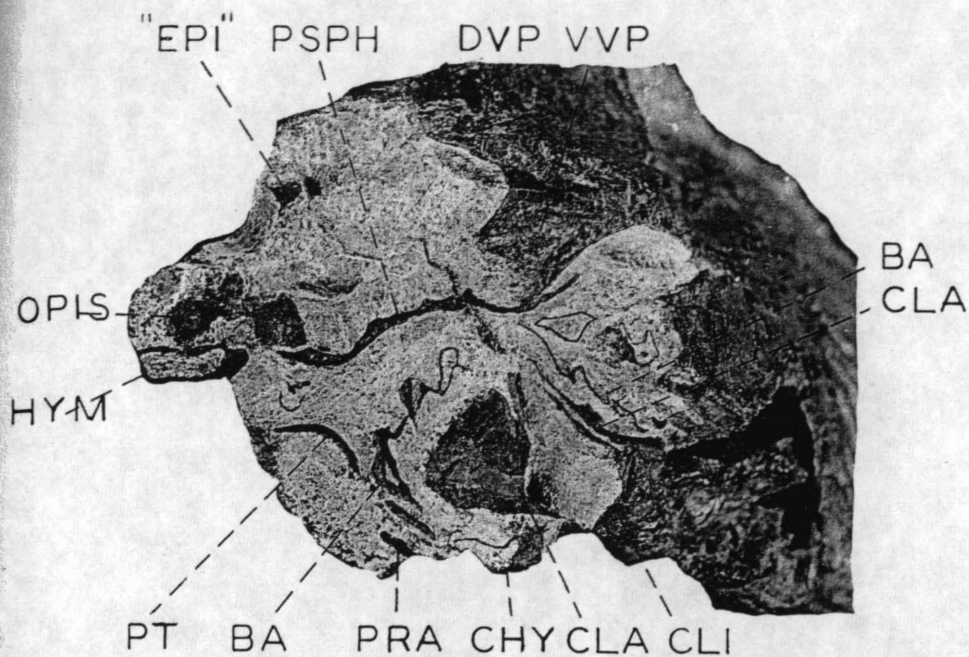VVP, ventral plate of the ventral process of the lateral extrascapula

PLATE IV

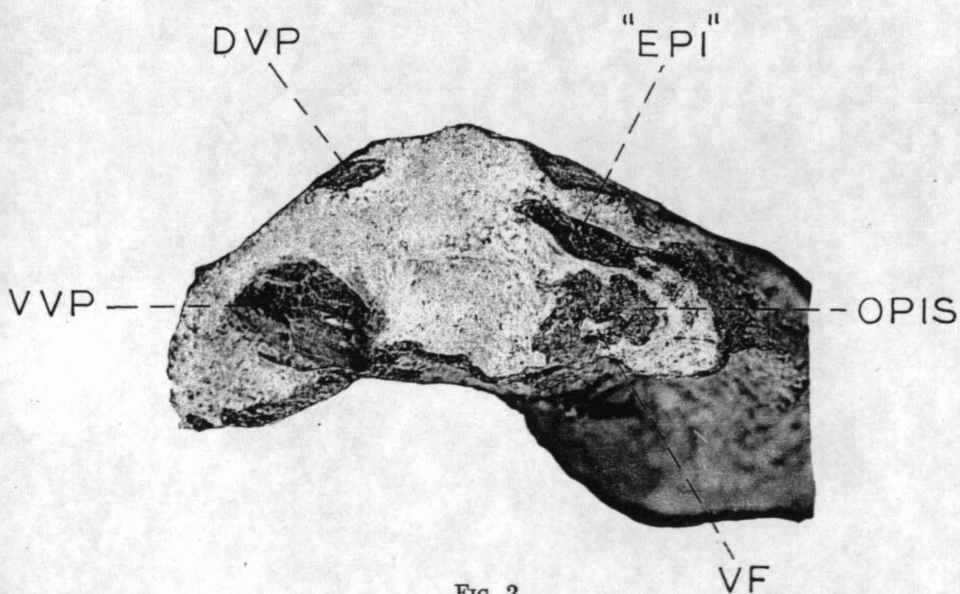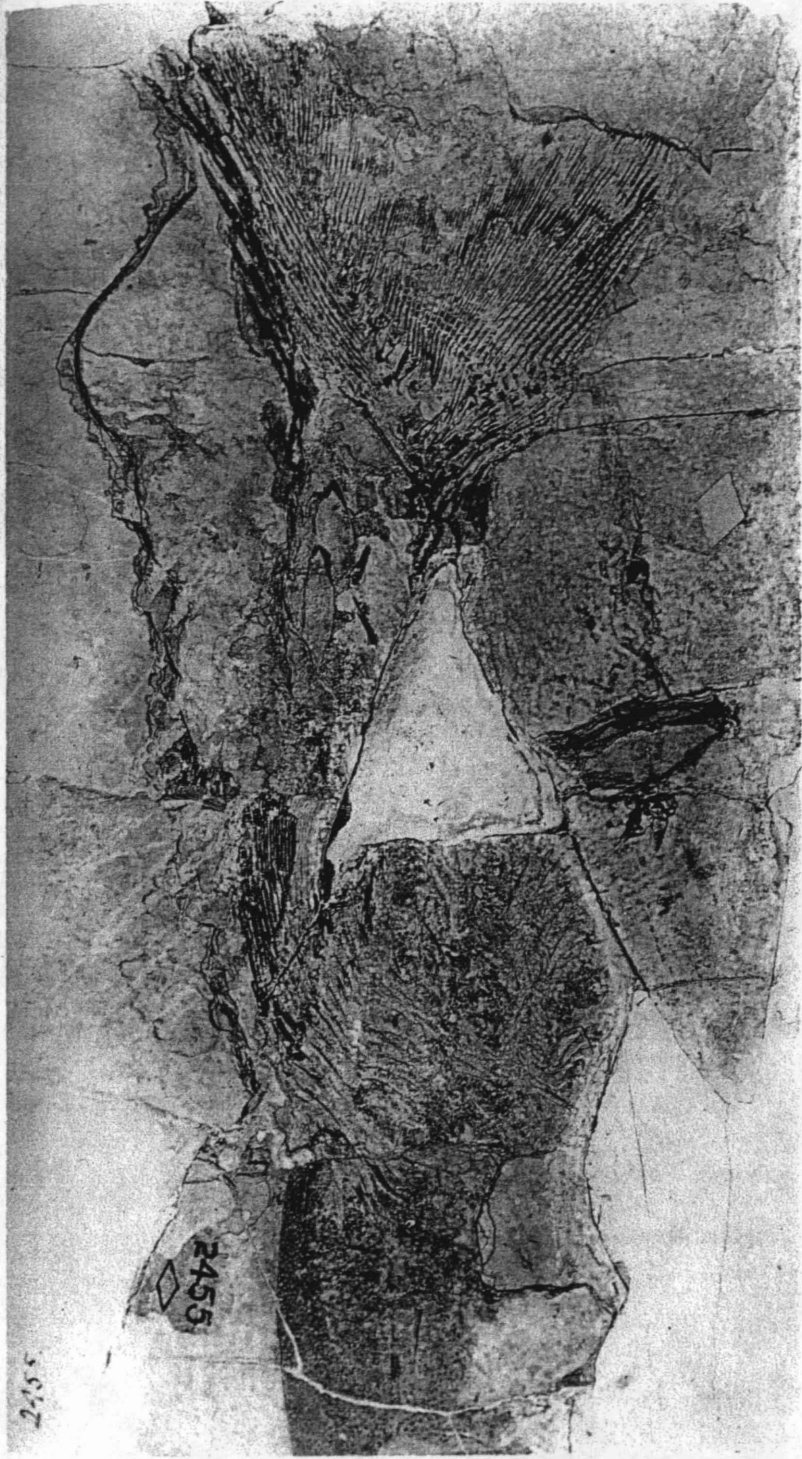"EPI" PSPH DVP VVP

BA
CLA

OPIS

HYM

PT BA PRA CHY CLA CLI

FIG. 1

DVP "EPI"

VVP OPIS

VF

FIG. 2

PLATE V

Crossopholis magnicaudatus. From the American Museum of Natural History, No. 2455. Posterior half of trunk. $\times \frac{2}{3}$

PLATE VI

Polyodon spathula, skin of trunk region just dorsal to anal fin. The photograph shows part of the main laterosensory canal and the scalelike pattern due to pigmentation. × 1⅔