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ABSTRACT

An entirely new group of Pennsylvanian fishes, belonging to the class Chondrichthyes, is described and their comparative anatomical and phylogenetic relations are discussed. Seven species belonging to five genera are distinguished and placed within the subclass Holocephali as a separate order, Iniopterygia. The iniopterygians are structural, but not phyletic, intermediates between the chimaeroids (as here defined) and the elasmobranchs. Present analysis permits the notion that the holocephalians and the elasmobranchs are sister groups sharing a common ancestor that never possessed a bony dermal armor but an even spread of lepidomorial denticles over the entire skin and the stomodaeum. Iniopterygians and chimaeroids, in turn, appear to be sister groups having evolved from a common ancestor that combined an autostylic jaw suspension with a generalized shark-like dentition.

Iniopterygians are presently known only from carbonaceous, sheety shales of the Pennsylvanian basin complex of central North America.

INTRODUCTION

Since 1954 when E. S. Richardson, Jr., and the senior author began an intensive study of the carbonaceous, sheety, black shales that overlie coal III-A in Parke County, Indiana (Mecca Quarry shale), it was quite obvious that among the hundreds of fish remains recovered from this deposit there were peculiar cartilaginous fishes clearly not identifiable as sharks. The head region and the post-cranial skeleton of these peculiar vertebrates consist of calcified cartilage and the dentition is made up of a considerable variety of teeth, sometimes fused into labio-lingual tooth whorls. Also, in some genera the mouth cavity is armored with large plates that consist of numerous, fused denticles.

As all specimens had been mutilated by predators (see Zangerl and Richardson, 1963) and therefore do not consist of skeletons in pristine condition, the morphology of these fishes remained a mystery for many years, in spite of the fact that more than a hundred specimens were at hand. Even those specimens that seemed to be relatively complete (and have since proved to be so) seemingly failed to fit into the structural plan of any primitive vertebrates presently known. For want of an identification and because they had tuberculated head plates, we called them "placoderms."

In the meantime, the junior author began to collect vertebrates from carbonaceous, sheety, black shales in Iowa and Nebraska. In the latter state he enjoyed the co-operation of local amateur collectors, primarily Mr. W. D. White and Mr. William Rushlau, both of Omaha, Nebraska. This collecting activity resulted in the preservation of numerous very important specimens including a variety of sharks and also the curious questionable vertebrates. In the fall of 1969 the junior author invited Dr. Barbara Stahl and the senior author to his home where he displayed his collection of vertebrates from several black shales of Iowa and Nebraska. A number of these skeletons resembled the "placoderms" of the Mecca fauna, although most of them did not display tooth whorls or large tuberculated plates. In contrast to the material from Indiana, these specimens did not appear to have been preyed upon and seemed to be in fair to excellent state of articulation. It was Dr. Stahl who broke the riddle by her observation that in several specimens (preserved in side view) the large, evidently paired fins just back of what appeared to be the head region, seemed to lie consistently on the dorsal side of the vertebral column and that they seemed to extend from the "nape" of the neck. The senior author then reviewed all of the best specimens from the Indiana localities and found that the dorsal position of the anterior paired fins is indeed evident in all laterally entombed individuals in which this region of the skeleton has been left undisturbed. It also became quite evident that many of the Indiana skeletons were more complete (and less disturbed) than had been assumed prior to the examination of the junior author's collection. An earlier suspicion that the material included not one, but several kinds of these peculiar fishes became increasingly apparent as the study of the material progressed. It was imperative that the junior author's collection of iniopterygians be studied along with the material from Indiana and he has graciously donated it to Field Museum. At the same time field work in Indiana, especially in the roof shale over coal IV-A in Pike County, Indiana, has furnished a large number of additional specimens.

The following account will provide a broad morphological characterization of a new order of vertebrates and the description and characterization of five genera and seven species, all of which, peculiarly, have escaped the recorded fossil record to date. Because of the nature of their preservation many aspects of their morphology remain to be determined in the future as additional (especially well-preserved) individuals are collected, a perfectly realistic hope in view of the fact that these animals are extremely abundant in a number of localities.

The illustrations are the work of G. R. Case, based on drawings and sketches by the senior author. Dr. Tibor Perenyi, staff illustrator at Field Museum, added some finishing touches to the illustrations.

The following persons have been members of Field Museum collecting parties since 1963: Mr. Orville L. Gilpin, Miss Gwendolyn Hall, Mr. Arthur R. Zangerl, and the senior author. We are also much indebted to Mrs. Winifred Reinders for her care with the manuscript and to Dr. Eugene S. Richardson, Jr., for the critical reading of the text. All radiographs were made with Siemens Heliodor-Duplex X-ray equipment fitted with a Pantix tube.

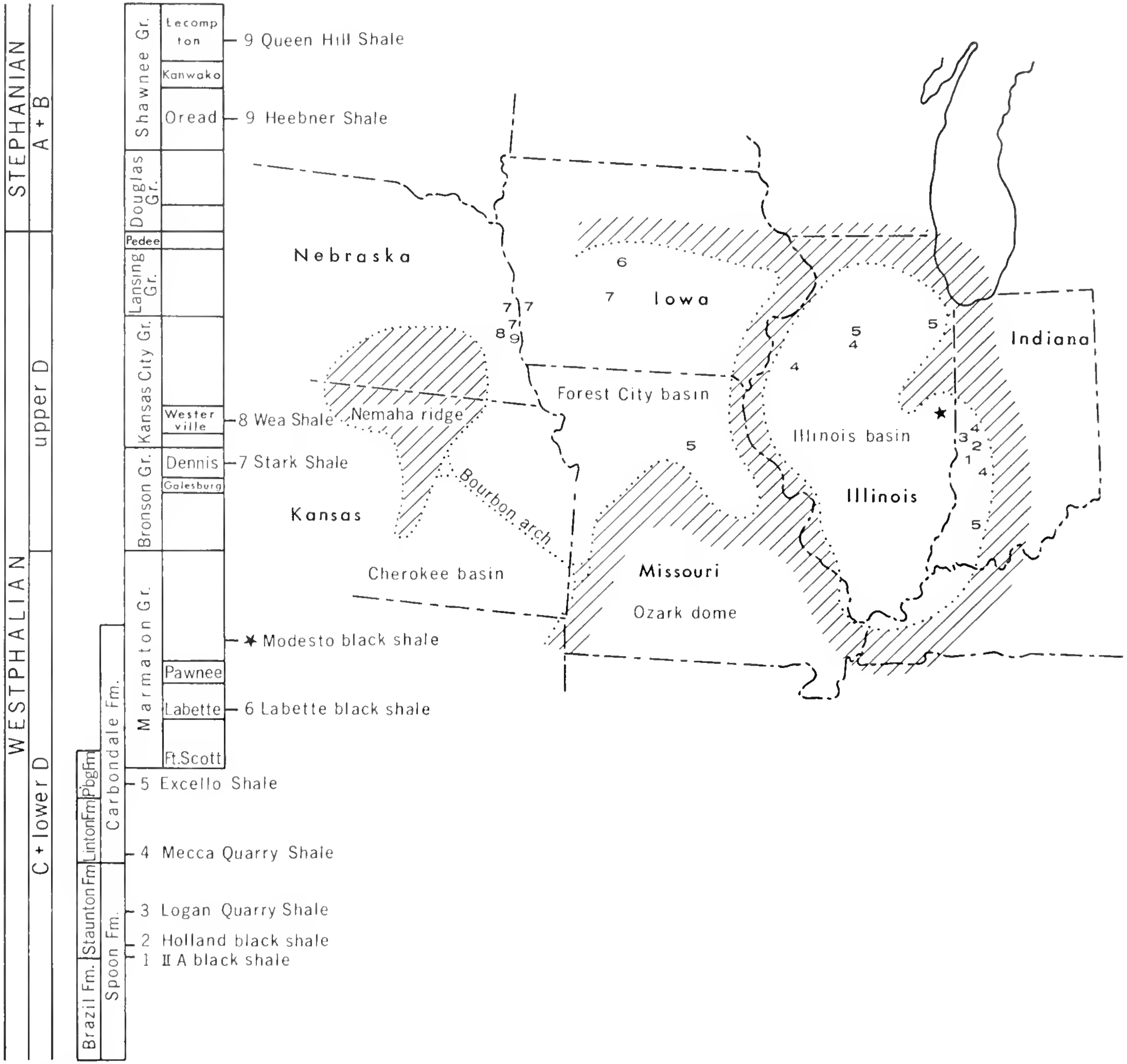

FIG. 1. Geographic and stratigraphic distribution of the black shale localities in which iniopterygians have been found. Correlation based on Kosanke et al., 1960, and Wanless, 1969.

LIST OF STRATIGRAPHIC BLACK SHALE HORIZONS AND LOCALITIES

The following is a list, in stratigraphic sequence from youngest to oldest, of the black shales that have produced iniopterygians and the localities from which they have come. This permits us to avoid the repetitious listing of this information for the referred specimens listed under each species below. The stratigraphic and geographic distribution of the localities is given in Figure 1.

Queen Hill shale, Lecompton formation, Shawnee group, Virgil series, Stephanian A, Pennsylvanian.

Plattsmouth, Nebraska, Cass County, Midwest Construction Co., Ace Hill E½ SW¼ SW¼ Sec. 33, T12N, R14E.

Stennett, Iowa, Montgomery County; Kaser Construction Co., Quarry, C NE¼, Sec. 27, T73 N, R38 W.

Wea Shale, Westerville formation, Kansas City group, Missouri series, Westphalian D, Pennsylvanian.

Papillion, Nebraska, Sarpy County; City Wide Rock and Excavation Co. (Hansen quarry, quarry 6), halfway between Papillion and Bellevue, Nebraska, on Route 370; SE¼ NE¼ SW¼, Sec. 32, T14N, R13E (fig. 2).

Richfield, Nebraska, Sarpy County, City Wide Rock and Excavation Co., PWA quarry (also known as Schmid quarry), S½ N½ Sec. 28, T13N, R12E, north of Platte River.

Stark shale, Dennis formation, Bronson group, Missouri series, Westphalian D, Pennsylvanian.

Crescent, Iowa, Pottawattamie County, Schildberg Construction Co., quarry, about 2 miles west of town, NE¼ NE¼ Sect. 34, T76N, R44W (Omaha North Quadrangle).

Ft. Calhoun, Nebraska, Washington County; Ft. Calhoun Rock Products Co., quarry, NW¼ NW¼ SE¼ Sect. 1, T17N, R12E.

Papillion, Nebraska, Sarpy County; City Wide Rock and Excavation Co. (Hansen quarry, quarry 6), halfway between Papillion and Bellevue, Nebraska, on Route 370; SE¼ NE¼ SW¼, Sec. 32, T14N, R13E.

La Platte, Nebraska, Sarpy County; City Wide Rock and Excavation Co., quarry (Iske quarry), River

FIG. 2. City Wide Rock and Excavation Co., Hansen quarry, June 1969. Wea shale exposed in headwall between Westerville limestone (above) and Winterset limestone beneath. Stark shale is almost at water level.

FIG. 3. Penn-Dixie quarry, Winterset, Iowa, April 1968. Stark shale exposed in middle foreground.

Road from Offutt Airbase, SW¼ SE¼ SW¼ Sec. 20, T13N, R13E and N½ N½ NE¼, Sec. 29, T13N, R13E.

Winterset, Iowa, Madison County; Penn-Dixie Cement Co. quarry, immediately southeast of town limits, W½ Sec. 6, T75N, R27W. (fig. 3).

Labette black shale, Labette formation, Marmaton group, Des Moines series, Westphalian D, Pennsylvanian.

Madrid, Iowa, Boone County; exposures of black shale along the Des Moines River, about 2.5 miles NW of Madrid, C NE¼ Sec. 33, T82N, R26W, Preston Branch Tributary of Des Moines River (fig. 4).

Excello shale, (equivalents: black shale over coal IV-A, Indiana; black shale over coal IV, Illinois), Carbondale formation, Des Moines series, Westphalian lower D, Pennsylvanian.

Barret Cemetery: strip mine headwall, NW ¼, Sec. 3, T3S, R7W (Augusta quadrangle), north of Barret Cemetery, Pike County, Indiana.

Bethel Church: strip mine headwall, about center of NW¼ of Sec. 3, T3S, R7W (Augusta quadrangle), about ¼ mile SE of Bethel Church, Pike County, Indiana (fig. 5).

Beaver Pond: strip mine headwall close to boundary between NW and SW ¼ of Sec. 10, T3S, R7W (Augusta quadrangle), about 1 mile south of Barret Cemetery, Pike County, Indiana.

Pit 12, Peabody Coal Co., Grundy County, Illinois.

Pit 14, Peabody Coal Co., Kankakee County, Illinois.

Mecca Quarry shale, Liverpool cyclothem (Linton formation), Des Moines series, Westphalian upper C, Pennsylvanian.

Mecca quarry: SW ¼ NE ¼ Sec. 29, T15N, R8W, about 1 mile from town of Mecca, Wabash Township, Parke County, Indiana (Zangerl and Richardson, 1963, pp. 28, 44, pl. 1, 2).

U.S. Highway 41: outcrop of Mecca Quarry shale along U.S. Highway 41, SE of Mecca Quarry (Zangerl and Richardson, 1963, p. 44).

Mine Creek: exposures of Mecca Quarry shale along Mine Creek, NE ¼, Sec. 29, T15N, R8W, Wabash Township, Parke County, Indiana (Zangerl and Richardson, 1963, pp. 7, 27, 44).

Montgomery Creek: Wabash Township, Parke County, Indiana (Zangerl and Richardson, 1963, pp. 27, 39, pl. 5).

Spencer Creek: Wabash Township, Parke County, Indiana (Zangerl and Richardson, 1963, pp. 7, 27).

West Montezuma: Clay City Pipe Co., Pit no. 3, NW ¼, Sec. 35, T16N, R9W, Vermillion County, Indiana (Zangerl and Richardson, 1963, pp. 40, 58).

Moorehead's Bank: SW ¼ SW ¼ SW ¼, Sect. 28, T17N, R9W, Vermillion County, Indiana (Zangerl and Richardson, 1963, pp. 7, 83).

Arketex: Arketex Ceramic Corp. Pit, SE ¼, Sec. 10, SW ¼ Sec. 11, T16N, R9W, Vermillion County, Indiana (Zangerl and Richardson, 1963, pp. 7, 63).

Chinook mine: Ayrshire Colliery, S of Staunton, Clay County, Indiana.

Otter Creek: near bridge of section road over creek, Sec. 25 and 30, T30N, R8W, north of Ehrmandale (Richter Cemetery), Vigo County, Indiana.

FIG. 4. Outcrop of Labette shale, along bank of Des Moines River near Madrid, Iowa.

FIG. 5. Black shale over coal IVA (Excello shale); Summer 1970; Bethel Church locality, Pike County, Indiana.

Jelliff: along Court Creek, SW ¼ SW ¼ Sec. 15, T11N, R2E (Galesburg quadrangle), NW of Knoxville, Illinois.

Logan Quarry shale, Lower Wiley cyclothem (Staunton formation), Des Moines series, Westphalian upper C, Pennsylvanian.

Logan Quarry: NE ¼ SW ¼ Sec. 9, T16N, R8W, Reserve Township, Parke County, Indiana (Zangerl and Richardson, 1963, pp. 7, 67, pl. 3).

Hajji Hollow: NE ¼ SE ¼ Sec. 5, T15N, R8W, Wabash Township, Parke County, Indiana.

SYSTEMATIC DESCRIPTIONS

Class Chondrichthyes

Subclass Holocephali

Order **Iniopterygia,** nov.

Characterization.—Cartilaginous fishes whose skeletons tend to calcify at an early ontogenetic age. General body habitus similar to modern chimaeroids. Palatoquadrate fused to neurocranium. Mouth terminal. Skin devoid of dermal denticles except in *Iniopera.* Dentition ranging from labio-lingual rows (tooth families) of individual, extremely simple denticles, to rows of individual denticles with side cusplets, to an amazing variety of tooth whorls (individuals of tooth families fused at their bases) producing a "heterodonty" unrivalled among fishes. Snout sometimes provided with tubercles. Mucous membrane denticles in the pharyngeal region of some forms, large plates consisting of fused denticles lining mouth cavity of others. Pectoral fins large, characteristically attached to the shoulder girdle elements near their dorsal ends. Anteriormost fin ray of pectoral fin usually enlarged in males, bearing sharp denticles. Pelvic fins much smaller than pectoral fins and consisting of short cartilage rays followed distally by ceratotrichia (so far seen only in *Iniopteryx rushlaui*). In males a variety of elaborate clasper mechanisms. Tenacular hooks present as in chimaeroids. Dorsal fin weak, consisting of a number of fin rays; in some specimens of *Iniopteryx* dorsally fused with one another. Tail fin small, circular in lateral view. Vertebral column consisting of paired, simple neurapophyseal cartilage rods and paired cartilage pieces (arcualia) beneath the notochord. Spiral membrane within spiral intestine coiled as in sharks with at least 14 turns instead of three as in modern chimaeroids.

So far, known exclusively from Pennsylvanian black, carbonaceous, sheety shales (and one specimen from a Pennsylvanian concretion of otherwise unknown locality and horizon) of Westphalian C to Stephanian A age of the midcontinent of North America.

Five genera and seven species are presently recognized, most of them typical members of the Mecca fauna (Zangerl and Richardson, 1963).

Family **Iniopterygidae,** nov.

Characterization.—Iniopterygia in which the dentition consists of individual teeth arranged in labio-lingual rows (tooth families) as in sharks (including symphyseal ones), and Meckel's cartilages are not fused at the symphysis.

Genera.—*Iniopteryx* and *Promexyele*

Genus **Iniopteryx,**[1] gen. nov.

Characterization.—Most generalized genus of the order. Skull without mouth plates. Dentition consisting of individual, tiny denticles, mostly simple-conical, more rarely with minute side cusplets, probably arranged in labio-lingual rows (tooth families) as in sharks. Symphyseal tooth rows above and below modified into tooth whorls with grossly enlarged tooth bases not fused to one another. Mucous membrane denticles in the region of the branchial arches. Vertebral column consisting of about 40 vertebrae, about 20 being prepelvic. Pectoral fin with large, squarish basal cartilage plate, and 11 or more finrays, the anteriormost of which is greatly enlarged. Near posterior edge of pectoral fin, cartilage rodlets oriented at right angles to the finrays, forming an aileron.

In males anterior fin rays of pectoral fins enlarged, each provided with sharp denticles, diminishing in size distad. Pelvic fin bases elongated-triangular, each bearing a double tenacular hook in the male. Clasper apparatus consisting on each side of a proximal rod followed by about a dozen short cartilage pieces that taper to a point posteriorly.

Type species.—*Iniopteryx rushlaui*, n. sp.

Iniopteryx rushlaui,[2] n. sp.

Type.—FMNH PF6678, ♂, well-preserved, articulated, nearly complete skeleton, lacking part of the skull.

Horizon and locality.—Stark shale, Dennis formation, Bronson group, Missouri series, Westphalian D, Pennsylvanian. From Limestone quarry, Ft. Calhoun, Nebraska. Collected by Mr. W. Rushlau of Omaha, Nebraska.

Referred specimens.—

WEA SHALE

RICHFIELD

PF6677, ♂, anterior half of skeleton in side view, (W. Rushlau)

PF6675, ♂, anterior half of skeleton, side view, (G.R. Case)

PF6674, ♂, whole skeleton in side view, (W.D. White)

PF6673, ♂, partial skeleton, (W.D. White)

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[1] From *inion*=nape, and *pteryx*=fin.

[2] Named after Mr. William Rushlau of Omaha, Nebraska, who has collected the holotype as well as other specimens of iniopterygians.

PF6669, —, isolated tail fin, (G.R. Case)
PF6667, —, isolated pectoral fin base, (G.R. Case)
PF6666, ♂, anterior half of skeleton, (W.D. White)
PF6676, ♂, partial skeleton, (G.R. Case)

Papillion

PF6643, ♂, articulated partial skeleton, lacking part of skull and tail, (W.D. White)
PF6644, ♂, partial skeleton, articulated, (W.D. White)
PF6683, ♂, partial skeleton, (G.R. Case)
PF6680, ♂, partial skeleton, (G.R. Case)
PF6682, ? ♀, disarticulated pectoral fin, showing proximally fused finrays, (G.R. Case)
PF6681, ♂, pectoral fin, (G.R. Case)
PF6752, ♂, partial skeleton, (W.D. White)
PF7128, ♂, partial skeleton, (W.D. White)
PF7123, ♂, partial skeleton, (W.D. White)
PF7126, —, disarticulated skull, (W.D. White)
PF7125, ♂, posterior half of articulated skeleton, (W. D. White)
PF7191, ♂, partial skeleton, (G.R. Case)
PF7167, ♂, disarticulated skeleton, (W.D. White)
PF7190, ♂, gastric residue containing this species, (W. D. White)
PF7170, ♀, anterior portion of articulated skeleton, (W.D. White)
PF7188,? ♀, disarticulated skeleton, (W.D. White)
PF7166, ♂, partly articulated skeleton, (W.D. White)
PF7189, ♂, anterior half of articulated skeleton, (W. D. White)
PF7145, ♂, skull and shoulder, (W.D. White)
PF7146, ♀, skull and shoulder, (G.R. Case)
PF7139, ♂, disarticulated skeleton, (W.D. White)
PF7133, —, jaws and teeth, (W.D. White)
PF7153, ♂, gastric residue, containing remains of this species, (G.R. Case)
PF7222, —, part of skull, (W.D. White)
PF7211, ♂, anterior half of articulated skeleton, (Eric Scott Shields)
PF7220, ♂, articulated skeleton lacking skull, (W.D. White)
PF7219, ♂, excellent braincase, definitely associated with elements of *I. rushlaui*, (W. D. White)

Stark shale

Ft. Calhoun

PF6672, ♂, articulated skeleton, (G.R. Case)
PF6761, ♂, articulated specimen, lacking pelvic area and tail, (W. Rushlau)
PF6671, —, isolated tail fin, (W.D. White)
PF6645, ♂, excellent skeleton in side view, lacking tail, (G. R. Case)
PF6646, ♂, excellent skeleton, nearly complete, (W.D. White)
PF6658, ♂, disarticulated specimen, (W. Rushlau)
PF6691, ♀, articulated skeleton, lacking skull and much of shoulder, (G.R. Case)
PF6648, ♂, anterior half of articulated skeleton, (G. R. Case)
PF6765, ♂, partial skeleton, (W.D. White)
PF7192, ♂, partial skeleton, (W.D. White)
PF6703, ♂, excellent skeleton in side view, lacking tail, (G.R. Case)
PF6647, ♂, anterior half of large specimen, (W.D. White)
PF6665, ♂, minced skeleton, (W. Rushlau)
PF6664, —, isolated tail fin, (W. Rushlau)
PF6754, —, isolated tail fin, (W.D. White)
U.N.S.M.[1] 2906, ♀, anterior half of articulated skeleton in dorso-ventral position, (Larry D. Martin)

La Platte

PF6649, ♂, disarticulated, partial skeleton, (G.R. Case)

Crescent

PF6679, ♂, gastric residue containing remains of this species, (G.R. Case)
PF7165, ♂, partial specimen, (W.D. White)

Papillion

PF7176, ♀, juvenile, partial specimen, (W.D. White)
PF7152, ♂, articulated skeleton, (W.D. White)
PF7132, ♂, pectoral fin, (W.D. White)
PF7181, ♂, partial skeleton, (W.D. White)

Winterset

PF6662, ♂, partial skeleton, (G.R. Case)

Excello shale

Barret Cemetery

PF6611, ♂, disarticulated remains of pectoral fins (XR[2]: Barret 24)

Logan Quarry Shale

Logan Quarry

PF6661, ♂, LQS level J, articulated skeleton, lacking tail fin (XR: LQ237)
PF6660, ♂, LQS level J, isolated pectoral clasper hooks XR: LQ228)

Hajji Hollow

PF6587, ♂, partly articulated skeleton, incomplete (XR: HH5)

Characterization.—Anterior finrays of pectoral fins in males much enlarged and provided with a single file of about 13 fishhook-shaped denticles, diminishing in size distad.

Description.—The largest skeletons (i.e., PF6678 or PF6645) are between 30 and 35 cm. in overall length.

U.N.S.M. = University of Nebraska State Museum.
[12] XR=X ray plate.

FIG. 6. Dorso-ventrally preserved specimen of *Iniopteryx rushlaui*, PF6646, showing features of the spiral intestine. See also Figures 7 and 8.

FIG. 7. *Iniopteryx rushlaui*, PF6646, region of spiral intestine enlarged to show remains of internal membrane.

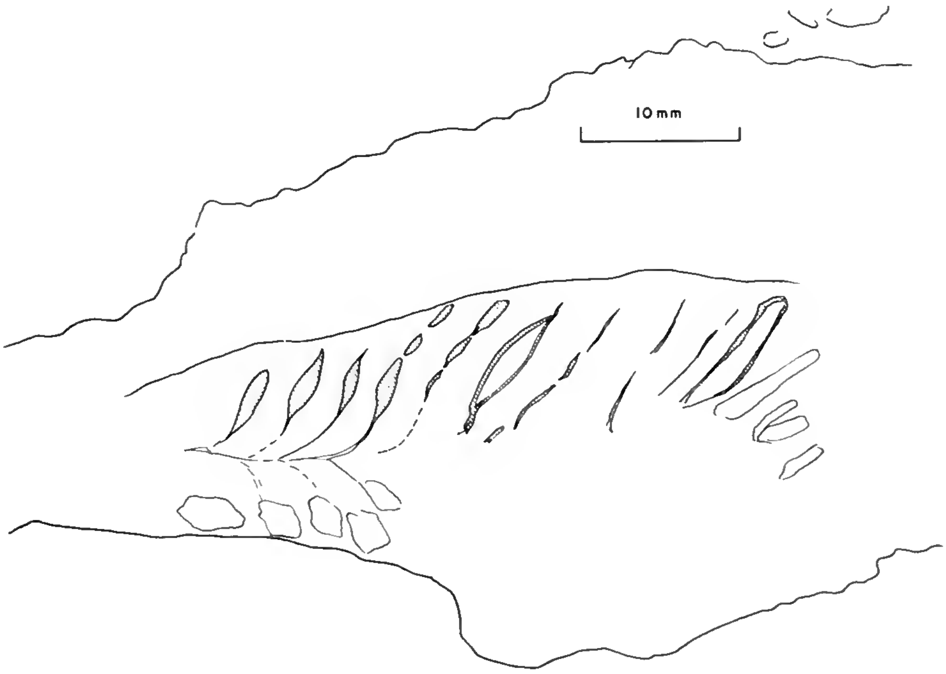

FIG. 8. Interpretation of photograph (fig. 7) of the remains of the spiral intestine of *Iniopteryx rushlaui*.

The combined skull and gill arch region of PF6645 measures about 7 cm. and the visceral portion of the body, back to the pelvic area, about 12 cm.

In a number of specimens (PF6645, PF6646 (fig. 6), PF6647, PF6761, and others) the abdominal cavity is filled with a light brownish, extremely fine-grained material that proved to be hydroxyapatite (with some calcite)[1]. The beige mass encloses the vertebral column which is preserved inside of it. In PF6672 and PF6646 this substance contains bits of arthropod exoskeleton, conodonts, and plant fragments. In PF6645 and especially in PF6646 the hydroxyapatite mass is bounded by a gray-bluish surface that shows darker bluish, diagonal stripes, and an extremely fine striated surface texture (figs. 7, 8). These structures are almost beyond doubt the casts of the inner surfaces of the spiral intestine, burst open following bloating, and the beige mass is gastric and/or intestinal content that oozed out of the digestive tube into the peritoneal cavity during the earliest phases of post-mortem bacterial degradation.

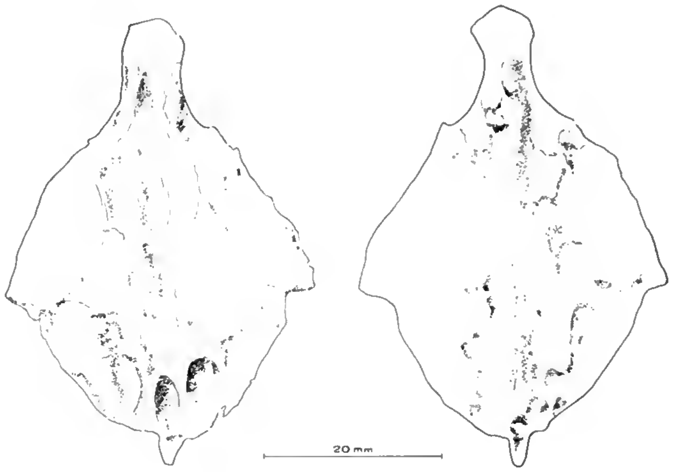

FIG. 9. Braincase of *Iniopteryx rushlaui*, PF2919, in dorso-ventral position. Plate and counterplate.

SKULL:

The present understanding of the skull and visceral skeleton of this species is very unsatisfactory, in spite of the fact that a large number of skulls is at hand. The specimens from Nebraska do not produce good radiographs, a fact that constitutes a major handicap. The neurocranium and visceral skeleton are invariably collapsed into a near two-dimensional layer of calcified cartilage and it is not possible to recognize with confidence the shapes and complexities of either.

In PF2919 the braincase is preserved isolated, in dorso-ventral position (fig. 9). However, the plate and counterplate do not show the dorsal and ventral surfaces of the neurocranium, rather the break lies near the presumed dorsal side. This is suggested by the fact that the counterplate shows a pronounced, rounded, sagittal ridge fitting into a corresponding groove on the plate side. This does not seem to be the proper relief for the base of the brain case. The nasal end of the neurocranium is narrow, bounded laterally by sharply defined, concave outlines that suggest that this denotes

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[1] Dr. Edward Olsen, Curator of Mineralogy at Field Museum kindly provided the analysis. The specimen analyzed was PF6645.

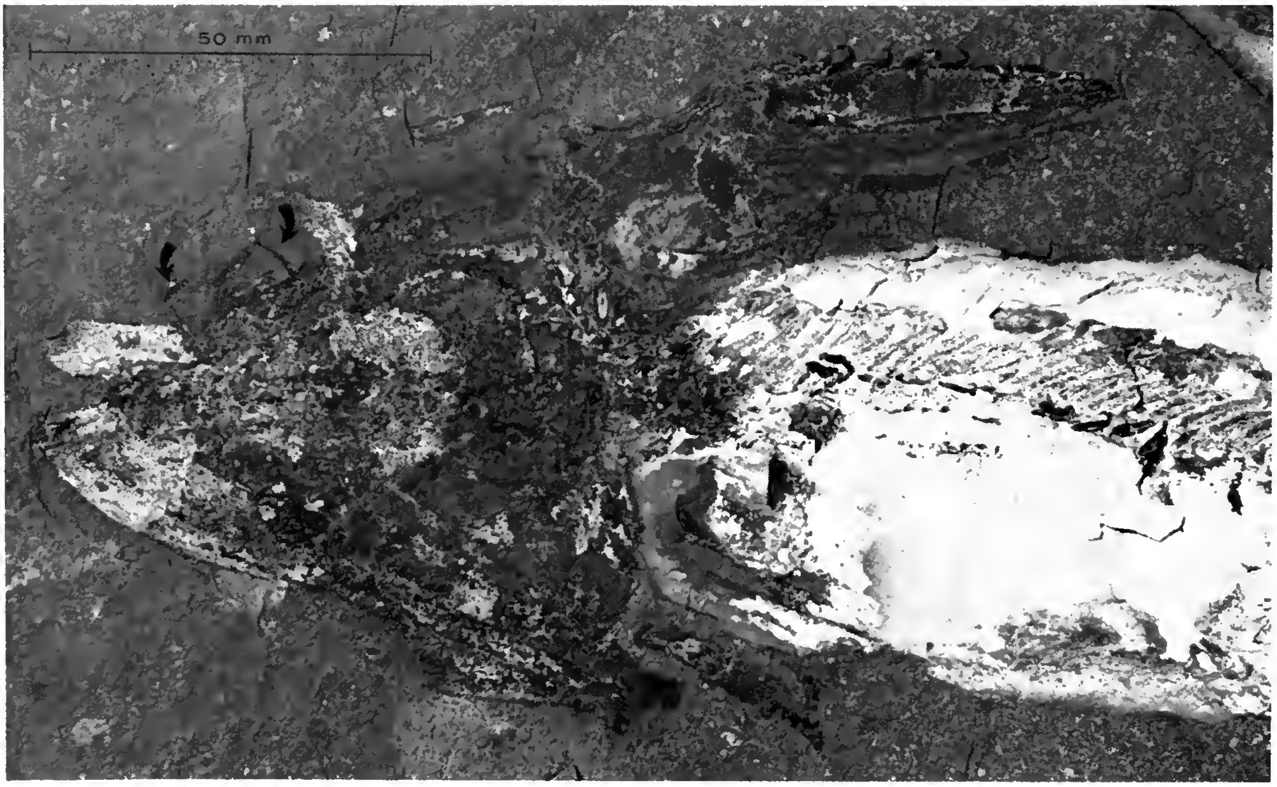

FIG. 10. *Iniopteryx rushlaui*, PF6645, anterior portion of skeleton preserved in side view. Arrows point toward enlarged calcified cartilage prisms that may have formed the rim of the orbit.

FIG. 11. *Iniopteryx rushlaui*, PF6675. Photograph of a polysulfide rubber cast (Smoothon) of the specimen in lateral position.

the position of the orbits. Slightly behind mid-length the neurocranium suddenly becomes much wider and that may be the place of articulation of the palatoquadrates with Meckel's cartilages, but well-defined articular facets are not developed as in *Iniopera* (fig. 61), for example. However, there is no evidence of separate palatoquadrates and it may be confidently stated that the skull is autostylic. There appear to be some striking differences between this braincase and the similarly preserved one of *Promexyele peyeri* (figs. 32, 33). But we are not yet able to state to what extent these apparent differences are due to the mode of preservation and the plane of splitting.

The size of the calcified cartilage prisms varies considerably in different parts of the skull of all iniopterygians, but in *Iniopteryx* there are rows of extra large prisms where one should expect the position of the eyes, and we thus assume that the rims of the orbits were

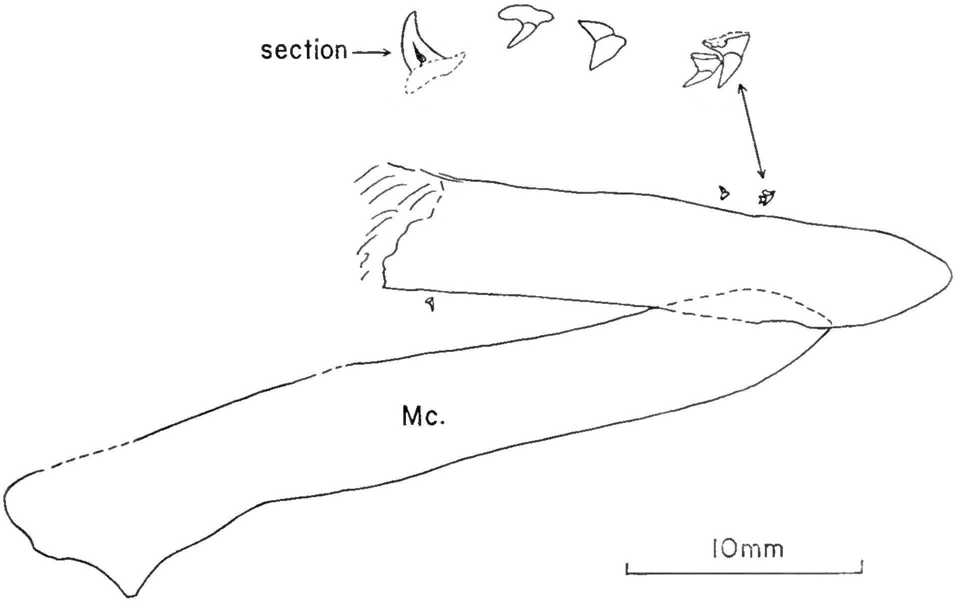

FIG. 12. *Iniopteryx rushlaui*, PF6761. Camera lucida drawing of Meckel's cartilages and a few teeth to show the size relationship.

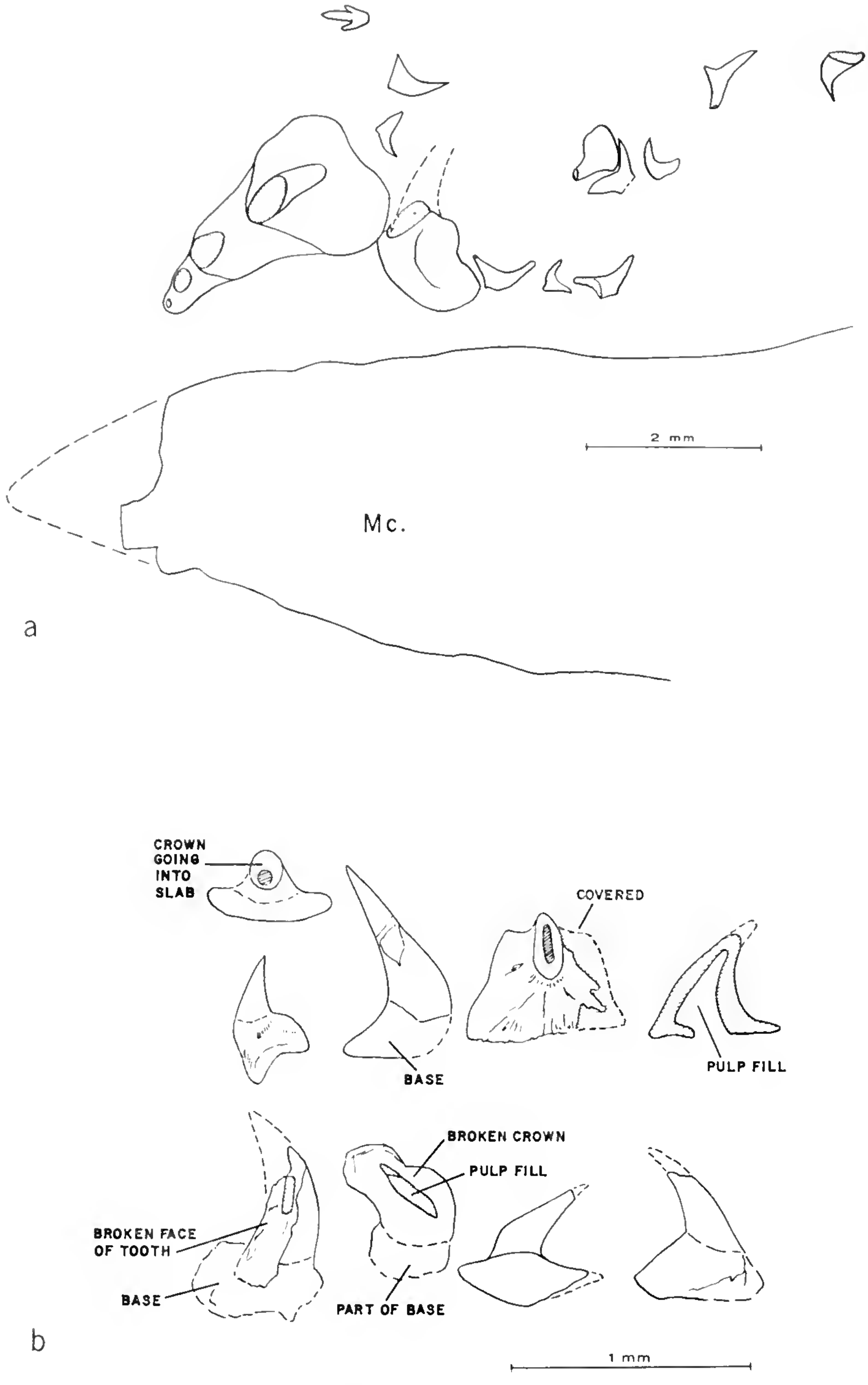

FIG. 13. Camera lucida drawings of jaw teeth of *Iniopteryx rushlaui*. **a**, PF6675, anterior end of Meckel's cartilage (Mc.) with the symphyseal tooth row above it and a scatter of side teeth; **b**, (top row) PF6658, a variety of teeth, including a symphyseal one to show morphological detail; (bottom row) PF6761, more posterior dentition teeth.

lined with these especially large calcifications (fig. 10). The Meckel's cartilages are rather slender rods, not fused at the symphysis (fig. 11).

The dentition is not preserved perfectly in place in any specimen. It is composed of a large number of individual, small, morphologically simple denticles, consisting of conical, slightly recurved crowns and somewhat expanded bases (fig. 12). Only rarely is a denticle seen that has tiny side cusplets (fig. 13). The dentine of the crowns looks solid and we presume that it consists of orthodentine. The pulp cavity is undivided and not filled with trabecular dentine (fig. 13). As may be seen from Figure 13, the size and the shape of the denticles vary considerably. At this time we are unable to differentiate teeth of the upper dentition from those of the lower jaw and there is good reason to believe that both upper and lower teeth are represented in Figure 13, and that differently shaped teeth belong to different tooth rows (tooth families) and/or different positions within the rows. Along the symphyses of

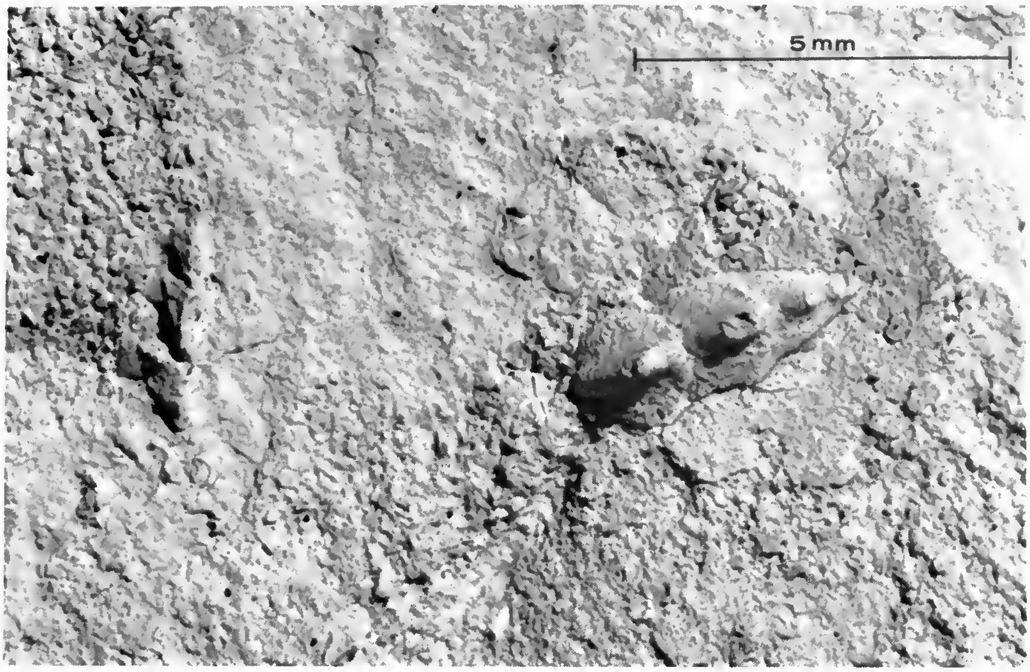

FIG. 14. *Iniopteryx rushlaui*, PF6645, photograph of polysulfide rubber cast (Smoothon) of the upper and lower symphyseal tooth rows.

both Meckel's cartilages and the palatoquadrates (presumed fused with the neurocranium) the sagittal tooth rows form tooth whorls of somewhat different shapes (figs. 13–15). Successive teeth—not fused to one another—in these whorls are of notably different size (fig. 13) indicating the rate of growth of these animals between the formation of successive tooth anlagen.

Well behind the areas where the mouth teeth are usually preserved in heaped accumulations and where one would expect the presence of pharyngeal gill arches, several specimens show additional accumulations of denticles. These denticles are usually in linear distribution which suggests that they were positionally related to the arches. The denticles that appear to belong to the same arch are of about the same size though there is some variation; based on this criterion there seem to be three pairs of gill arches that carry denticles, the anteriormost bearing the smallest denticles, the most posterior one the largest (fig. 16). From the position of the largest mucous membrane denticles relative to the entire head region it seems safe to say that they belong to the last pair of arches, and that the last three pairs bore denticles. But it does not necessarily mean, of course, that *Iniopteryx* had only three pairs of such

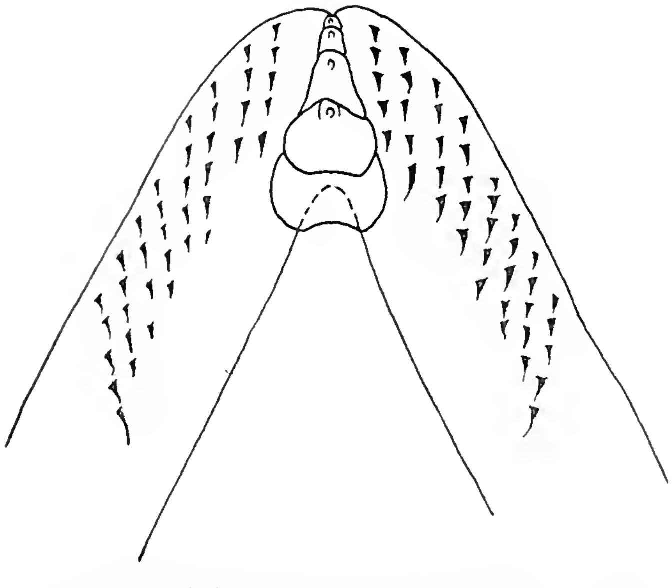

FIG. 15. Semi-diagrammatic illustration of the lower dentition of *Iniopteryx rushlaui*, as presently interpreted.

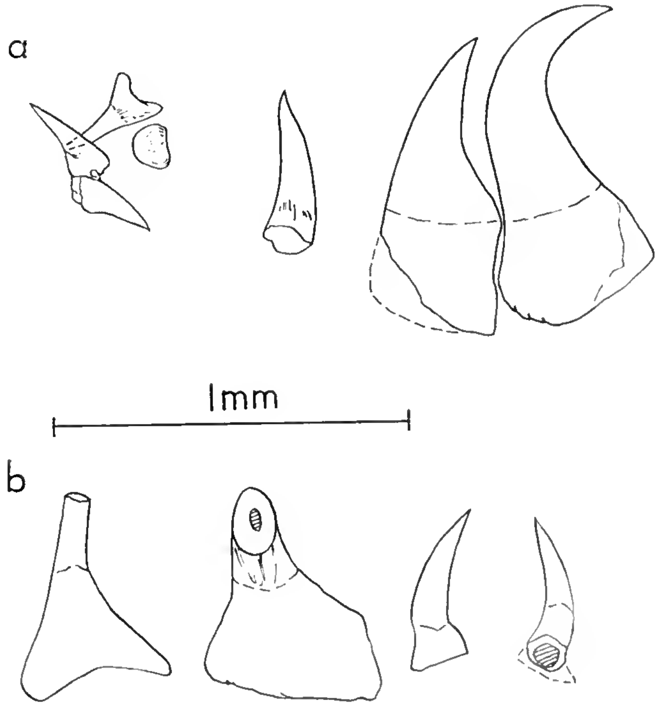

FIG. 16. Camera lucida drawings of mucous membrane denticles of ?gill area of *Iniopteryx rushlaui*. a, PF6645; b, PF6646, showing denticles of presumably different gill arches, see text.

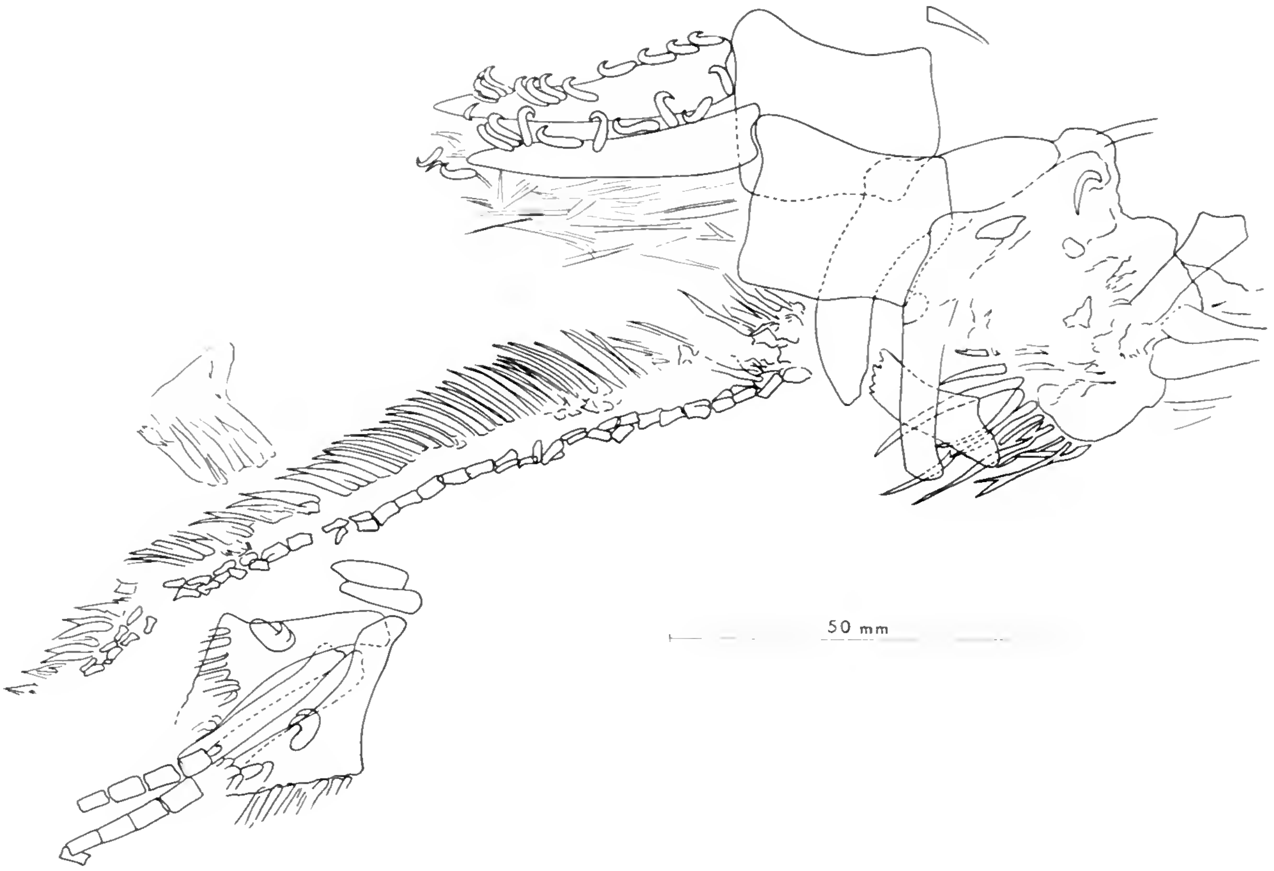

FIG. 17. *Iniopteryx rushlaui*, PF6661. Drawing made from enlarged stereo radiographs.

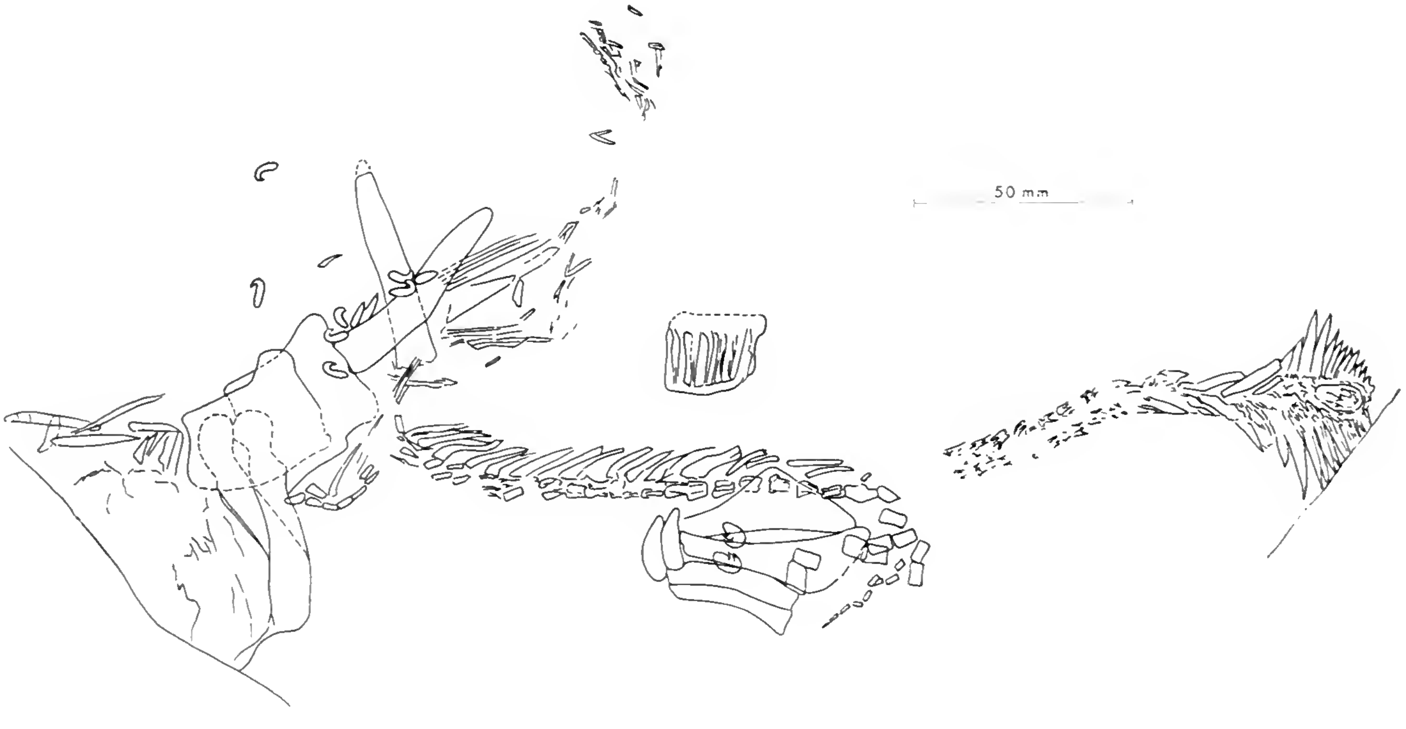

FIG. 18. *Iniopteryx rushlaui*, PF6678, holotype. Drawing made from enlarged photograph of the plate (fig. 20).

FIG. 19. Photograph of *Iniopteryx rushlaui*, PF6678, holotype, counterplate.

FIG. 20. Photograph of *Iniopteryx rushlaui*, PF6678, holotype, plate (see also fig. 18).

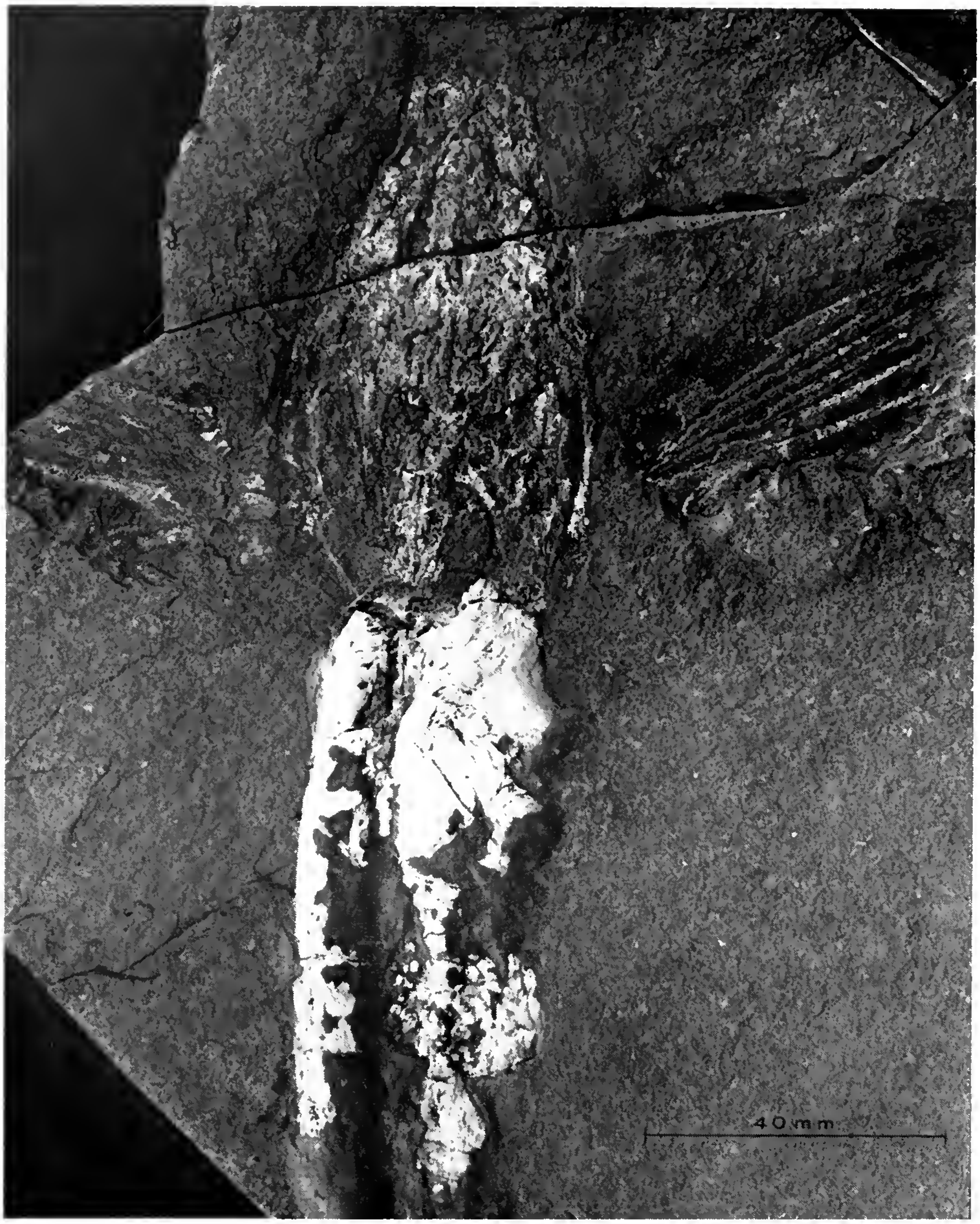

FIG. 21. *Iniopteryx rushlaui*, U.N.S.M. 2906, a female specimen in dorso-ventral position. Note moderate enlargement of first pectoral finray and absence of "fishhooks" alongside of it.

elements. At this time the full complement cannot be determined.

In PF6646 there are a few fairly large denticles so located in the specimen that it seems unlikely that they belonged to either the mouth dentition or the last pharyngeal arches. They might have been attached to the mucous membrane of the palate or to a basibranchial element.

In several specimens, but most impressively displayed in PF6677, PF6661, PF7170, and PF7181, there are six to ten calcified cartilage rays extending from the ventral side of the skull after the fashion of fin rays and pointing postero-ventrad (fig. 17). These cartilages increase in size backwards and, considering the skull as a whole, are relatively large. It cannot be determined what relation they have to other elements of the head region, but the most reasonable interpretation is that they are hyoid radials associated with the opercular flap as in chimaeroids. If so, they are relatively larger in *Iniopteryx* and not fused proximately.

VERTEBRAL COLUMN:

A minimum of 40 segmental units comprise the vertebral column and about half that number constitute the tail peduncle and the tail fin. One can clearly distinguish a row of dorsally pointed, elongated cartilage pieces that occupy the position of neural arches. Ventral to them there is often a vacant space (figs. 17, 18), presumably denoting the position of the notochord. Ventral to this space there is another antero-posterior row of paired, small, subrectangular cartilage pieces. These are in proper position for ventral arcuals. As in modern chimaeroids, there are no vertebral centra. The condition differs from that in chimaeroids by the fact that successive elements of dorsal and ventral arch pieces in the row are of the same size and shape; no distinction can be made between basidorsals and interdorsals per segmental unit as in chimaeroids (e.g., Schauinsland, 1903; Dean, 1906; Rauther, 1933; and Patterson, 1965, in the case of the fossil chimaeroid *Squaloraja polyspondyla*). In *Iniopteryx* there is, in fact, no evidence that dual elements per vertebral unit exist; rather, it seems that each vertebral element consists of a pair of dorsal arch pieces (neural arches) and a pair of ventral arcualia. The notochord remained entirely uncalcified. In the region of the tail peduncle both the dorsal and ventral arcualia are much smaller than in the thoracic region of the column and they appear to be somewhat incompletely calcified and hence are not distinctly outlined (figs. 18–20). Just anterior to the tail fin, however, there are again much larger cartilage pieces that may or may not be fin rays (fig. 18). The vertebral column extends to the very tip of the caudal fin where there is a larger, oblong piece of cartilage that may represent a fusion of arcualia (fig. 18).

SHOULDER GIRDLE AND PECTORAL FINS:

The shoulder girdle consists of two fairly stout elements immediately behind the gill area, curved in such a way that the ventral ends extend a little distance forward beneath the throat region (fig. 17). Near the dorsal ends of these cartilage pieces and on their posterior faces there are convex joint facettes for the articulation of the basal plates of the pectoral fins. In PF6661, drawn from enlarged stereoscopic radiographs, the joint processes appear to be located almost at midlength of the shoulder girdle pieces but this may not be the correct interpretation of the complicated shadow picture. It is not certain that the portion above the joint processes is as long as indicated in Figure 17. The element here described is best interpreted as a scapulocoracoid such as is found in sharks and chimaeroids; the right and left halves are not fused in the midline. Attached to the scapulocoracoids are two large squarish basal cartilage plates that bear the finrays (figs. 17, 18). The shape and size of these basal cartilage plates are characteristic for the genus *Iniopteryx*. At their antero-ventral corners they bear a shallow notch for the attachment to the articular knob on the scapulocoracoids. Diagonally across the plate, at the postero-dorsal corner, there is an articular knob to which the first (in swimming position the anteriormost), enlarged fin ray is attached. The fin is a most remarkable structure embodying features that are (to our knowledge) unique among vertebrates. The enlarged first fin ray is moderately enlarged in females (fig. 21),[1] strongly enlarged in the males where it bears a single file of 13 (several, though not all, specimens yield this exact count) fishhook-shaped denticles (figs. 17, 22). The recurved parts of the "fishhooks" face forward and the tubular bases (fig. 22) seem to be embedded, at least partially, in the cartilage of the finrays (fig. 17). Each fishhook denticle contains a simple pulp cavity, surrounded by a relatively thick coat of orthodentine. The crowns are glossy, probably covered with a thin layer of vitrodentine. Next to the enlarged, first finray there are a minimum of ten (PF7032) slender ones, decreasing in length and diameter slightly toward the last (fig. 22). At the (functionally) posterior side of the fin there are also structures that have no homologs or analogs in any other fishes: tiny calcified cartilage rodlets that extend from two or three posterior finrays and at about right angles to them toward the posterior margin of the fin (fig. 22). Some of these rodlets appear to be branched and we cannot be certain that they all originate from the same finray. Functionally, these rodlets perhaps served the same function as the structural skeletons within ailerons on airplane wings.

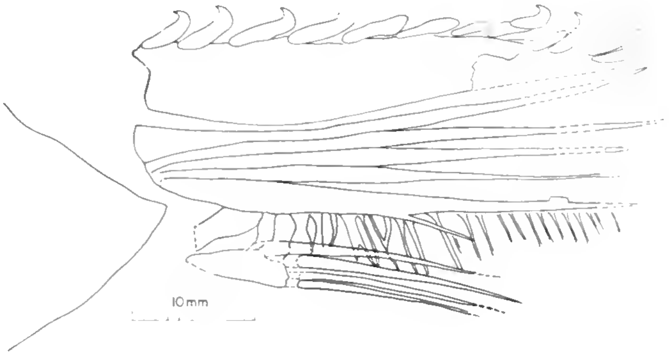

FIG. 22. Camera lucida drawing of pectoral fin of *Iniopteryx rushlaui*, PF7032, showing an exceptionally complete fin with the transversal struts near the posterior edge of the fin (see also fig. 10).

PELVIC GIRDLE AND PELVIC FINS:

The pelvic girdle consists of two rather featureless pieces of cartilage (figs. 17, 18, 23) that are not likely to have been in contact with one another ventrally. Attached to each of these small pelvic elements is a relatively large, subtriangular plate, the basipterygium that bears the finrays of the pelvic fin. The basipterygium also consistently bears a large double "fishhook" denticle (figs. 17, 23) which no doubt served as tenaculum. In chimaeroids the tenacular hooks are located on a ventro-lateral process of the pelvic element. The pelvic finrays, at least nine in number, are short and distally followed by ceratotrichia (fig. 24).

The condition of the pelvis in females (which are exceedingly rare in the collection) is not known. The clasper apparatus of *Iniopteryx rushlaui* consists of a pair of elongated, proximal cartilage rods followed by 15 or more consecutive, short cartilage pieces on each side that taper to a point posteriorly (figs. 17, 18, 23). Each clasper is evidently attached to the antero-medial edge of the basipterygium. There are no clasper hooks at the distal ends of the clasper structures.

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[1] At this point it is not possible to distinguish female specimens of *I. rushlaui* from those of *I. tedwhitei*. Since *I. rushlaui* is very much more common than the other species, it seems probable that the specimen illustrated in Figure 21 belongs to *I. rushlaui*, but there is no certainty.

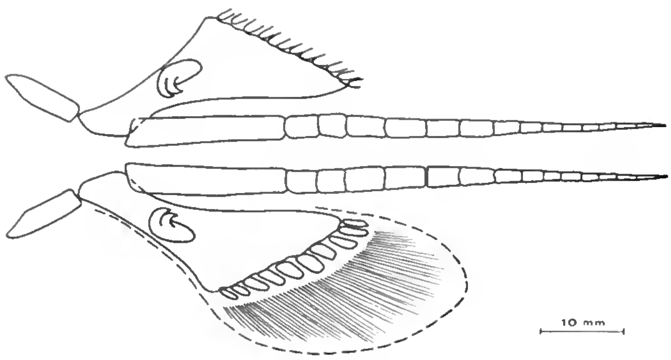

FIG. 23. Reconstruction of pelvic complex of a ♂ *Iniopteryx rushlaui* showing pelvic fin with short finrays and ceratotrichia as seen in PF7125 (see fig. 24).

UNPAIRED FINS:

The dorsal fin is located dorsal to the pelvic region (figs. 18, 20). It consists of about six finrays that are dorsally fused into a sagittal cartilage plate. There may also be fusion of the rays proximally, as for example, in the type specimen PF6678 (fig. 18).

The caudal fin is nearly circular in side view (figs. 18, 25). About 15 functional finrays form the dorsal lobe and about an equal number form the ventral lobe. In the posterior region of the tail peduncle there are a dorsal and a ventral series of cartilage pieces resembling small finrays that seem to grade into the tail fin. Between the dorsal and ventral finrays there is a mass of cartilage pieces whose shapes are not discernable, and the center of the posterior half of the caudal fin is formed by an oval cartilage plate (see p. 17).

The morphological interpretation of this caudal fin is obviously difficult since the involvement of the arcualia of the vertebral column cannot be made out in the present material. A conservative interpretation would compare this fin with the caudal of one of the Paleozoic sharks in which the dorsal lobe consists of the modified arcualia that accompany the notochord, and the ventral lobe consists of cartilaginous fin radials. With this model in mind one would identify the dorsal functional finrays as modified neurapophyses, the indistinct cartilage elements and the terminal, oval plate as modified ventral arcualia. The ventral finrays would be homologous to the radials in the ventral lobe of the shark caudal fin.

APPEARANCE IN LIFE:

In Figure 26 we have attempted to give an idea of what *Iniopteryx rushlaui* may have looked like in life. In overall habitus (though not in any details) *Iniopteryx* resembled *Chimaera*: head higher than wide and relatively large; thorax ovoid and fairly sharply set off against the tail peduncle; large pectoral fins and relatively large pelvic fins; tail fin symmetrical; skin naked (though in chimaeroids there are dermal denticles along the sensory lines). Beyond these rather broad similarities *Iniopteryx rushlaui* differed in appearance very much from all modern and fossil chimaeroids. The most striking feature is the attachment of the pectoral fins high up on the shoulder girdle; the morphology of the fins strongly suggests that the pectorals were held horizontal and at a right angle to the main axis of the body (fig. 27). The tail fin probably was no larger than the distal ends of the finrays indicate to judge by the finray relationship in the tails of sharks like *Cladodus* or *Cladoselache*. The dorsal fin of *Iniopteryx* was probably supported by the dorsal, fused part of the basal fin elements and may have been fleshy or membranous above it. In life the rims of the orbits may have been fairly prominent and the gill region was covered by membranous flaps supported by cartilage rods, much as in modern chimaeroids.

Functional matters.—The relative size of the pectoral fins and their position high up on the side of the body indicate that this pair of fins was the principal locomotor organ. The articulation of the large basal cartilages with the shoulder girdle elements leaves little doubt that the fins were moved vertically rather than fore and aft, possibly much as in the cheloniid sea turtles: in both cases the flipper (or fin) has a sturdy anterior edge and a thin, flexible posterior fringe. In the sea turtles

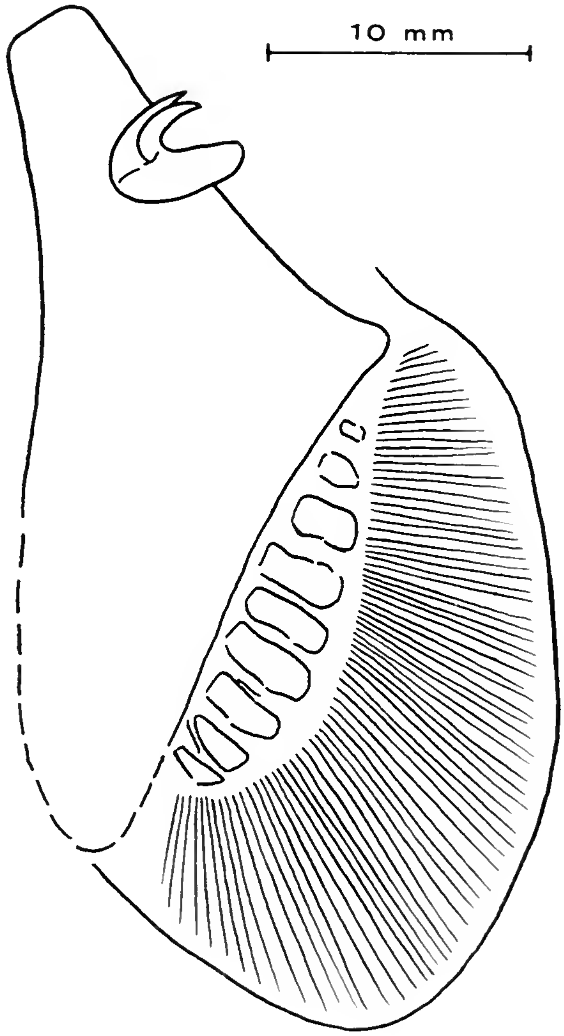

FIG. 24. Camera lucida drawing of pelvic fin of *Iniopteryx rushlaui*, PF7125, showing ceratotrichia.

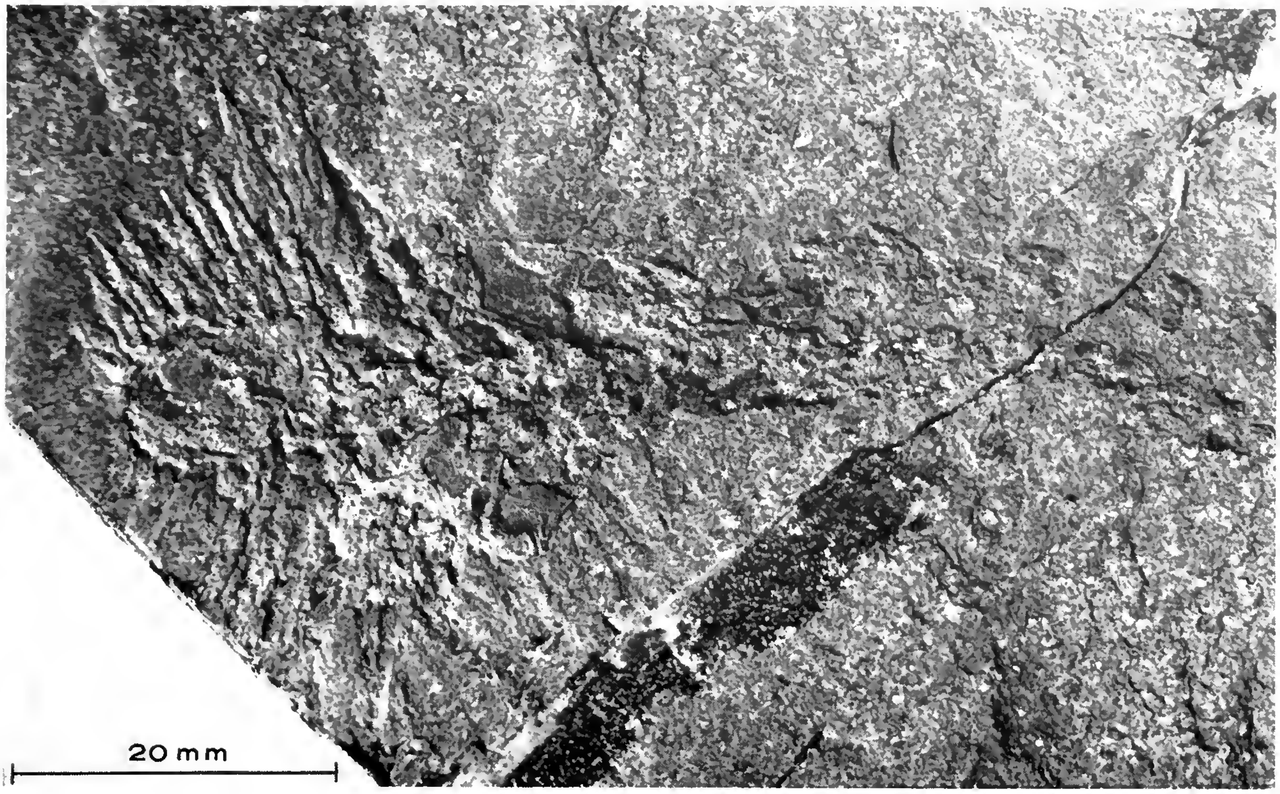

FIG. 25. Enlarged tail fin of *Iniopteryx rushlaui*, PF6678, counterplate.

there is a certain amount of axial rotation of the flipper during the downstroke and upward recovery; the same was most likely true of the fin of *Iniopteryx*, to judge from the position of the scapular attachment facette of the basal fin cartilage at its postero-medial corner (fig. 26). The large cartilage plate, and especially its anterior part, very probably served for the insertion of powerful muscles both dorsally and ventrally that originated on the shoulder girdle and could effect not only a downstroke, but also an axial rotation of the fin such that its stiff anterior edge was lower than the posterior edge during the downstroke, and reversed relations during upward recovery (fig. 28). The tail fin was most likely used during slow swimming and propelled the animal by the usual lateral motions of most fish tails. During faster propulsion, by means of the pectoral fins, the tail almost certainly served for steering. The dorsal fin and the pelvic fins probably acted as stabilizers.

Food.—The stomach and/or intestinal contents of several specimens contain remains of arthropods, conodont "denticles," and plant remains. The dentition of *Iniopteryx rushlaui* consists of such delicate denticles that the animals probably could not cope with anything other than soft-bodied food.

Sex ratio.—Of 56 specimens in which the sex can be determined, only seven are females and two of these are doubtful. The reason for this disparity is almost certainly predation (see Zangerl and Richardson, 1963). It seems probable that the males with their series of forward looking hooks along the first finrays of the pectoral fins could hold the fins at a right angle to the body axis thus discouraging all but the largest predators from engulfing them whole, while the unarmored females could be subdued much more easily.

Geographic, stratigraphic and paleoecological relations.—*Iniopteryx rushlaui* is a member of the Mecca fauna (Zangerl and Richardson, 1963; in press) and a beautifully articulated skeleton (PF6661) comes from the Logan Quarry shale in Parke County, Indiana. Most of the specimens, however, have been found in stratigraphically higher black shales in localities around Omaha, Nebraska. These black shales are sandwiched between massive limestones and the paleogeographic circumstances of their deposition undoubtedly differed from those of the Mecca or Logan Quarry shales in Indiana. Their origin, as flotant sediments (Zangerl and Richardson, 1963), on the other hand, was probably the same.

The Stark and Wea shales in eastern Nebraska, on the whole, tend to be limier than the black sheety shales that overly coals (e.g., the Mecca and Logan Quarry shales in Indiana) and it is at least possible that *Iniopteryx rushlaui* preferred a more carbonate-rich habitat. This conclusion is mildly supported by the fact that iniopterygians of other genera are barely more abundant in these shales and localities than is *Iniopteryx* in Indiana. The presently known stratigraphic range of this species is Westphalian C to Westphalian upper D (fig. 1).

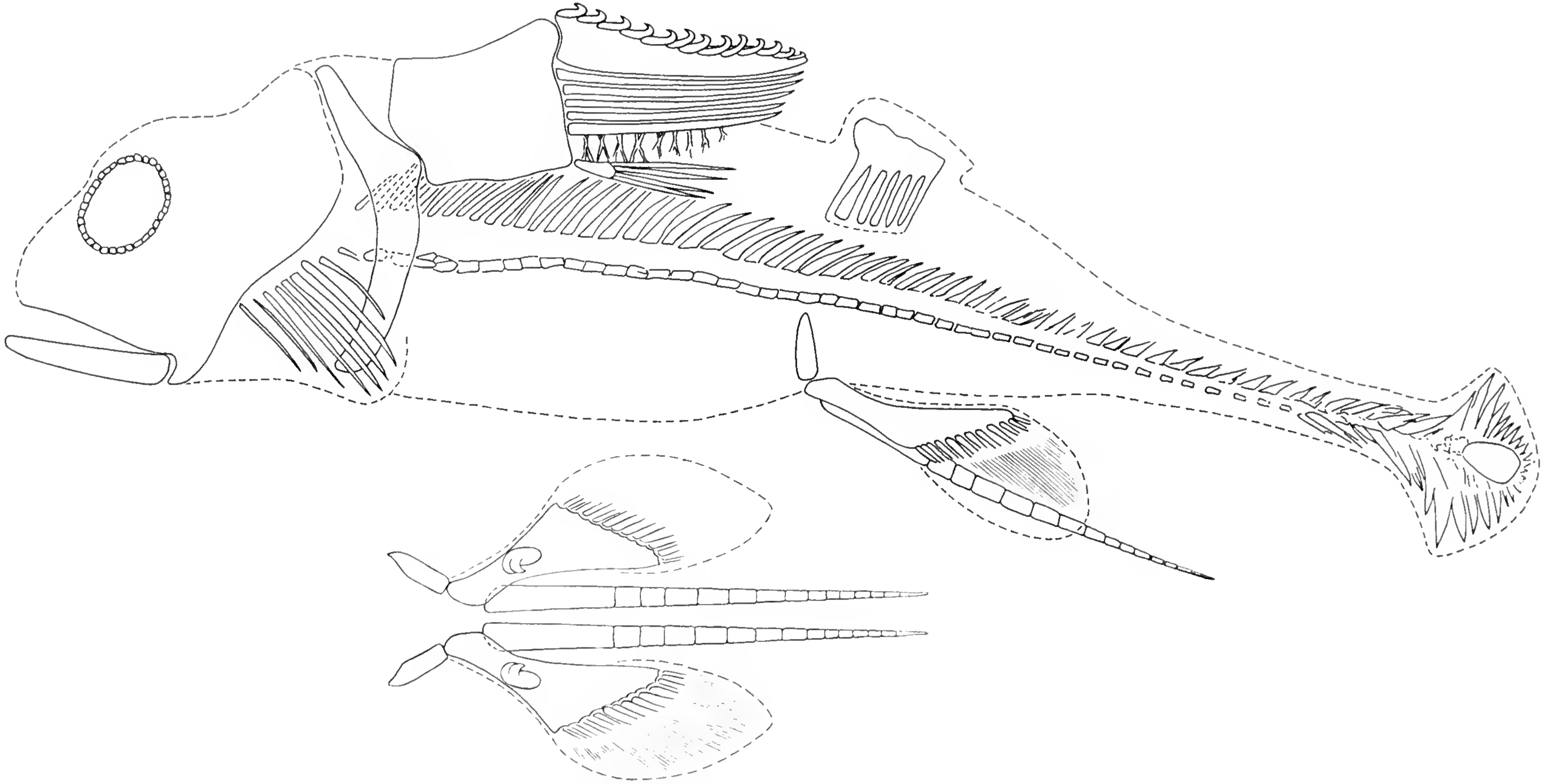

FIG. 26. Reconstruction of skeleton of *Iniopteryx rushlaui* in lateral view; based on a number of specimens. Below, the pelvic region of the ♂ in ventral view.

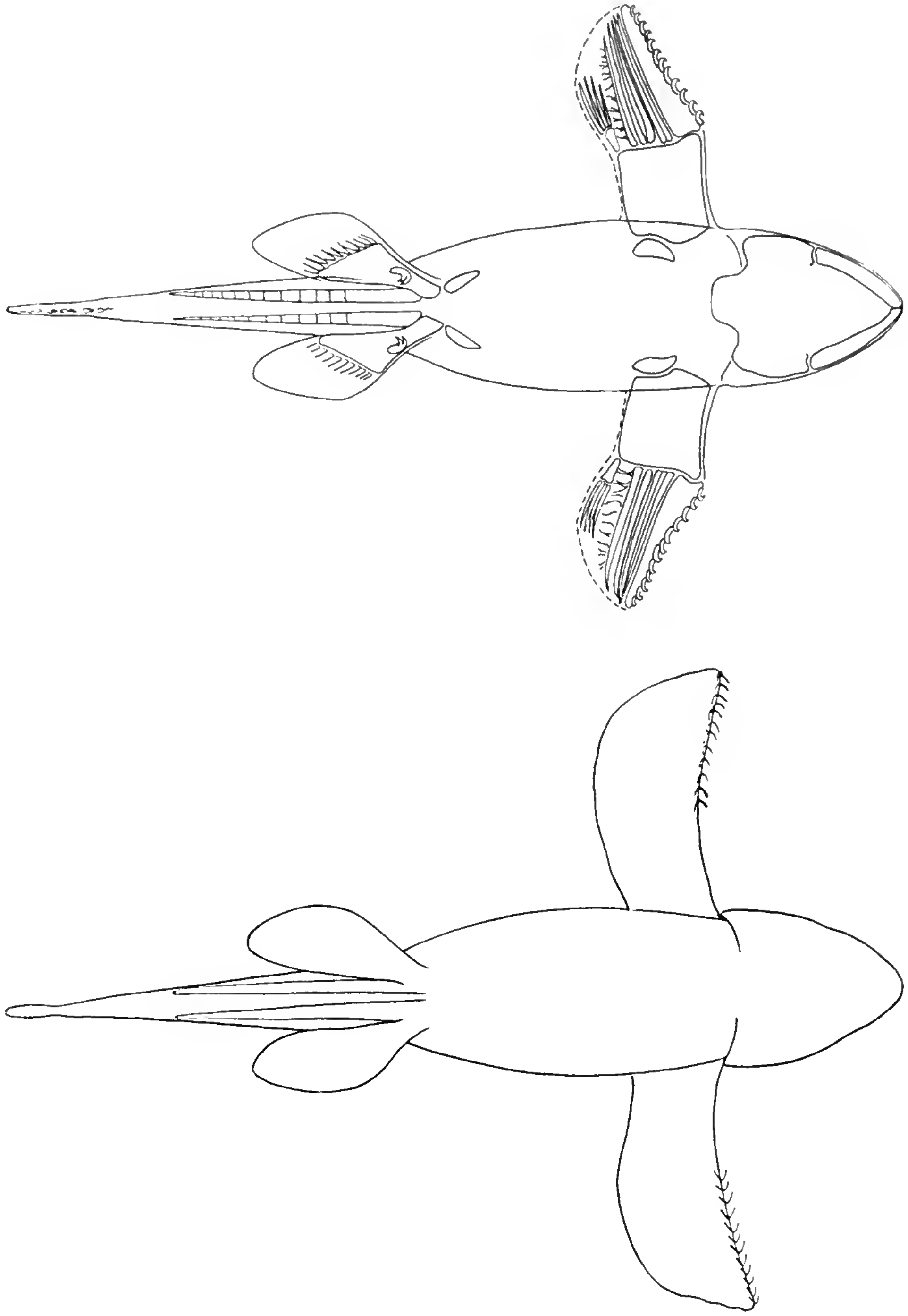

FIG. 27. Presumed body outline in ventral view of *Iniopteryx rushlaui* showing (top) our interpretation of the normal position of top pectoral fins during locomotion; (bottom) possible defense or threatening position of the pectoral fins.

Iniopteryx tedwhitei,[1] n. sp.

Type.—FMNH PF7241, ♂, articulated skeleton lacking tail region and clasper mechanism.

Horizon and Locality.—Wea shale, Westerville formation, Kansas City group, Westphalian D, Pennsylvanian; Papillion, Nebraska; collected by Mr. W. Rushlau, 1970.

Referred specimens.—

Wea shale

Papillion

PF6709, ♂ skeleton lacking skull and shoulder-girdle, (W.D. White)

Richfield

PF6753, ♂, part of a skeleton, (W. Rushlau)

Stark shale

Papillion

PF7202, ♂, partial skeleton, (W. D. White)

PF7242, ♂, good skeleton, (W. D. White)

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[1] Named for Mr. W. D. White of Omaha, Nebraska, the most avid collector of iniopterygians.

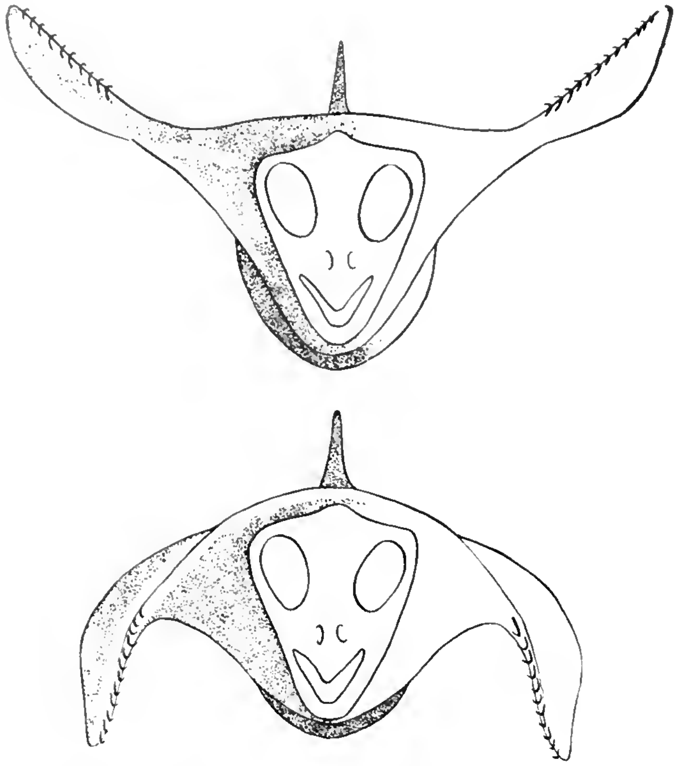

FIG. 28. Assumed swimming positions of the pectoral fins of *Iniopteryx rushlaui* (see text).

WINTERSET

PF5900, ♂, part of skeleton showing rasp hooks

Characterization.—Anterior finrays of pectoral fins in males moderately enlarged and covered by several rows of denticles with very much enlarged bases and straight (not recurved) crowns. Denticles diminish in size distad.

Description.—The rasp denticles of this species are so distinctly different from those of all other iniopterygians, and especially from those of *Iniopteryx rushlaui*, that in the absence of other features, one would not consider this a species of *Iniopteryx*. The skulls of the type specimen and of PF7242 show, however, that the dentition consists of simple, individual denticles, exactly as in *I. rushlaui* (fig. 15) and the enlarged symphyseal denticles appear also to be the same. Furthermore, the type specimen shows the typical, enlarged calcified cartilage prisms, that probably formed the rims of the orbits in the genus (fig. 29).

The rasp denticles—one cannot call them "hooks"—consist of slender, straight crowns and very much enlarged, saddle-shaped bases (fig. 30). On the fin rasp they point backward (as preserved) and may have pointed backward and outward in life. In PF7241 the skin of the rasp that held the denticles evidently sloughed off during degradation and flattened out near the body so that the denticles in this specimen form patches of pavement. Other specimens show clearly, however, that these are not dermal denticles of the body skin, but that they are, indeed, attached to the first ray of the pectoral fin forming a rasp.

None of the presently available skeletons of this species add to the knowledge of the genus. *Iniopteryx tedwhitei* appears to be far less common than *I. rushlaui*, and there are no specimens of *I. tedwhitei* from localities in the Illinois basin. At the present time female specimens of this species cannot be distinguished from those of *I. rushlaui*, thus it is not entirely impossible that some of the female individuals listed under *I. rushlaui* actually belong to this species.

Genus **Promexyele**,[1] gen. nov.

Characterization.—Generalized iniopterygians. Dentition consisting of individual teeth with two side cusplets each that probably stand in labio-lingual rows (tooth families) as in sharks; bases of these teeth slightly expanded beyond crowns and very rough beneath. Enlarged symphyseal tooth rows present, but not well known. Vertebral column, so far as known, similar to *Iniopteryx*. Pectoral fin very long, with much smaller fin base cartilage (basipterygium) than in *Iniopteryx*; six or more finrays with the first (anteriormost) enlarged in males and studded with hook-shaped denticles that have enlarged bases and decrease in size distad. Pelvic basipterygia triangular, little elongated. Multiple tenacular hooks (in males) on either side, apparently attached to separate cartilage pieces.

Type species.—*Promexyele peyeri*, n. sp.

Promexyele peyeri,[2] n. sp.

Type.—FMNH PF5911, somewhat disarticularted ♂ skeleton, lacking some of the skull. XR: Moorehead's Bank No. 1

Horizon and locality.—Mecca Quarry shale, Liverpool cyclothem (Linton formation), Westphalian C, Pennsylvanian. Moorehead's Bank, along Little Vermillion River, Vermillion County, Indiana. Collected June 1, 1961.

Referred specimens.—

LABETTE BLACK SHALE

MADRID

PF6657, –, partly disarticulated anterior portion of skeleton, (G. R. Case)

EXCELLO SHALE

BETHEL CHURCH

PF6495, —, partial skull, XR: Bethel No. 10

PF7116, ♂, partial skeleton, small individual

PF6516, —, small, partial skeleton

PF6522, —, head region of small individual. XR: Bethel No. 30

PF6497, —, partial skeleton, XR: Bethel No. 12

PF6555, —, partial skeleton, very small individual XR: Bethel No. 47

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[1] From *promeces*=elongated, and *xyele*=rasp.

[2] Named in honor of the late Professor Bernhard Peyer, who had a lifelong interest in teeth and dentitions of lower vertebrates.

FIG. 29. Camera lucida drawing of *Iniopteryx tedwhitei*, PF7241 (holotype).

MECCA QUARRY SHALE

MECCA QUARRY

PF2815, ♂, anterior half of skeleton in fair articulation Mecca quarry, level A1.2; XR: MQ 171

PF2916, ♀, anterior half of skeleton in fair articulation Mecca quarry, level A1.2; XR: MQ 59

PF6724, —, gastric residue mass containing teeth and tooth plates of *Promexyele*. Mecca quarry, level A4.4

CL 153, ♀, anterior half of fairly large individual. From a lateral extension of the original Mecca quarry, dug by Mr. John Carlson. XR: MQ 01

JELLIFF

PF5896, ♂, skull and pectoral region in fair articulation, XR: Jeliff No. 4

LOGAN QUARRY SHALE

LOGAN QUARRY

PF2358, ♀, excellent anterior half of skeleton. Logan quarry, level J; XR: LQ 207.

PF2510, —, small, disarticulated head region. Logan quarry, level J

PF6636, —, partly articulated head and shoulder region. XR: LQ 33

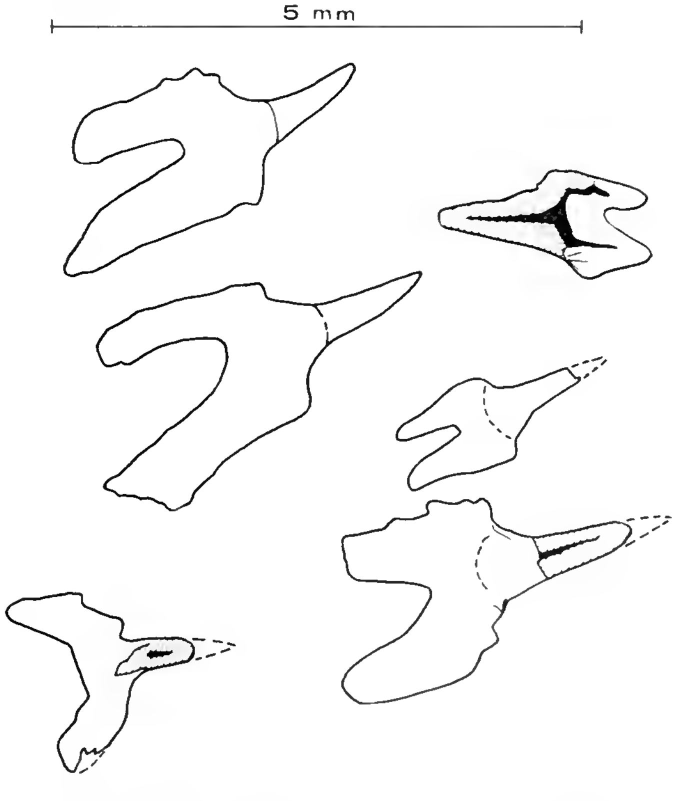

FIG. 30. Camera lucida drawing of the rasp denticles of *Iniopteryx tedwhitei*, PF5900.

FIG. 31. Tracing from enlarged photographs and radiographs of the skeleton of *Promexyele peyeri*, PF5911 (holotype). **a,** black: both pectoral fins; shaded, anterior to pectorals: head region; shaded, posterior to pectorals: probably elements of the dorsal fin. **b,** black: shoulder girdle; shaded: pelvic elements and clasper apparatus.

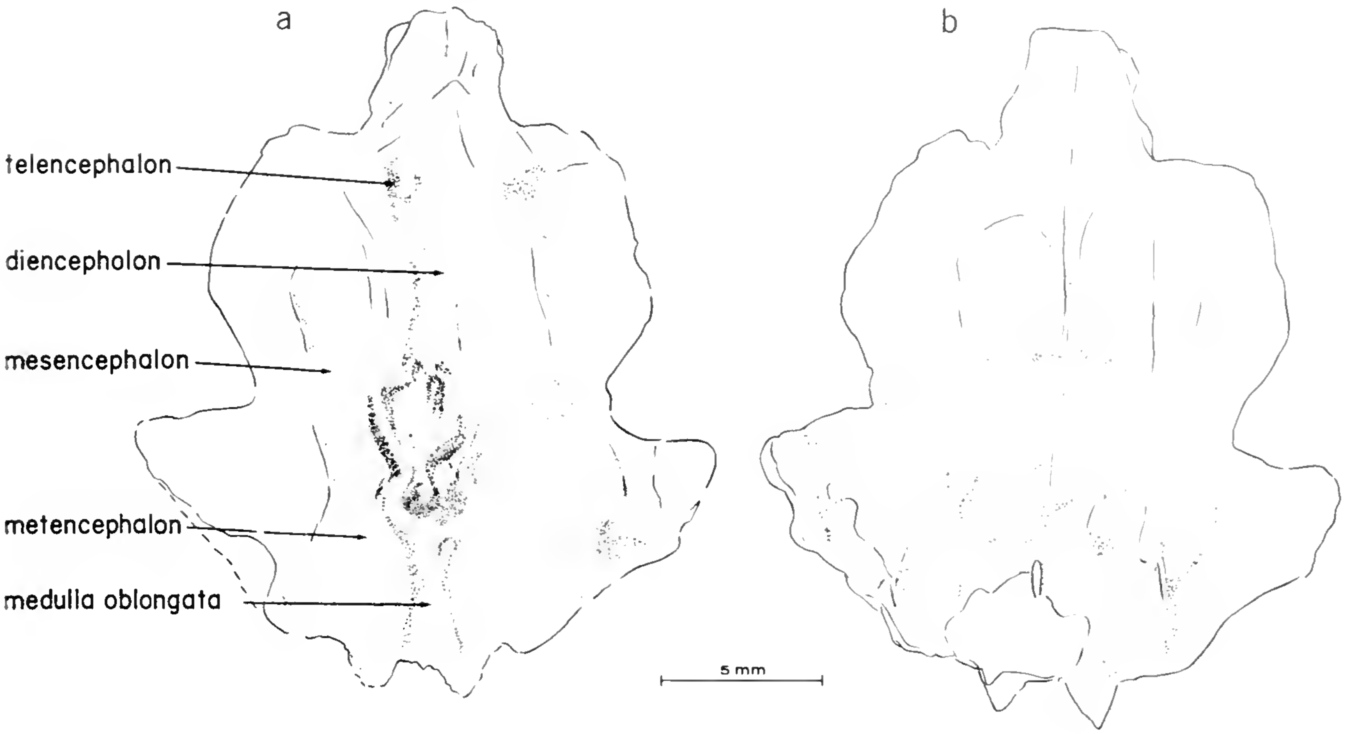

FIG. 32. Drawings of braincase (**a**, plate and **b**, counterplate) of *Promexyele peyeri*, PF6578, using different directions of illumination (see also fig. 33).

PF2364, ♀, partial skeleton in fair articulation. Logan quarry, level J; XR: LQ 168

Characterization.—First fin rays of pectoral fins very much elongated and studded with hook-shaped denticles with large bases (150 plus, on either side). Three tenacular double hooks in males on either side. Clasper apparatus consisting on each side of about five short cartilage segments, followed by an elongated rod bearing minute clasper hooks at the end.

Description.—None of the specimens recognized as *Promexyele peyeri* are sufficiently complete to permit the description of the overall habitus and body proportions of this species. Compared to *Iniopteryx rushlaui* the pectoral fins are relatively longer (fig. 31) and possibly narrower and in males the first rays are much more heavily armored with hooks—in fact, these rays might be described as rasps. Also clearly different in appearance from those of *Iniopteryx*, are the pelvics of *Promexyele peyeri*: they are relatively shorter, perhaps broader, and the copulatory apparatus has a different construction.

The skull is hardly better known in this animal than in *Iniopteryx*. There are similarities in the fact that Meckel's cartilages were free anteriorly and relatively weak elements. In PF6578 there is a braincase in dorso-ventral position, divided on plate and counterplate in such manner that we see the inner dorsal and ventral surfaces of the brain capsule. The relief on these two surfaces is, of course, minimal, but present and quite interesting. It is also difficult to interpret, because comparable views of neurocrania of modern chondrichthyans seem to be utterly lacking in the literature. The shape of this braincase (fig. 32) shows from front to back a relatively narrow rostral section, large bulbous expansions in the region of the eyes, pronounced processes of the fused palatoquadrates for the articulation of the Meckel's cartilages, and an occipital region that is characterized by two posterior projections on either side of the presumed position of the foramen magnum. In the gross features mentioned this braincase conforms to a number of other iniopterygian braincases, though few of them show the bulbous expansions in the orbital region. The surface relief of the two halves has been emphasized in the drawings (fig. 32). As the photographs (fig. 33) clearly show, most of this relief consists of fairly undisturbed surfaces of calcified cartilage prisms which means that we are looking at the dorsal and ventral interior wall surfaces of the brain case, but it is by no means easy to decide which is the dorsal, which the ventral side. The relief on the plate is a trifle more complex than that on the counterplate. It consists of a fairly well-defined, sagittal depression extending from the position of the presumed foramen magnum a short distance forward where it divides into the narrower depressions that surround a circular structure (fig. 32a) and immediately in front of that a somewhat larger, approximately circular area. In front of the latter there is once more a fairly wide, median depression which seems to widen noticeably at its forward end (fig. 32a). Between the median structures described and the articular facettes on the fused palatoquadrates there are other elements of surface relief that are probably associated with the auditory capsules. If the relief features in the median plane are related to the morphology of the brain, as would seem reasonable, one

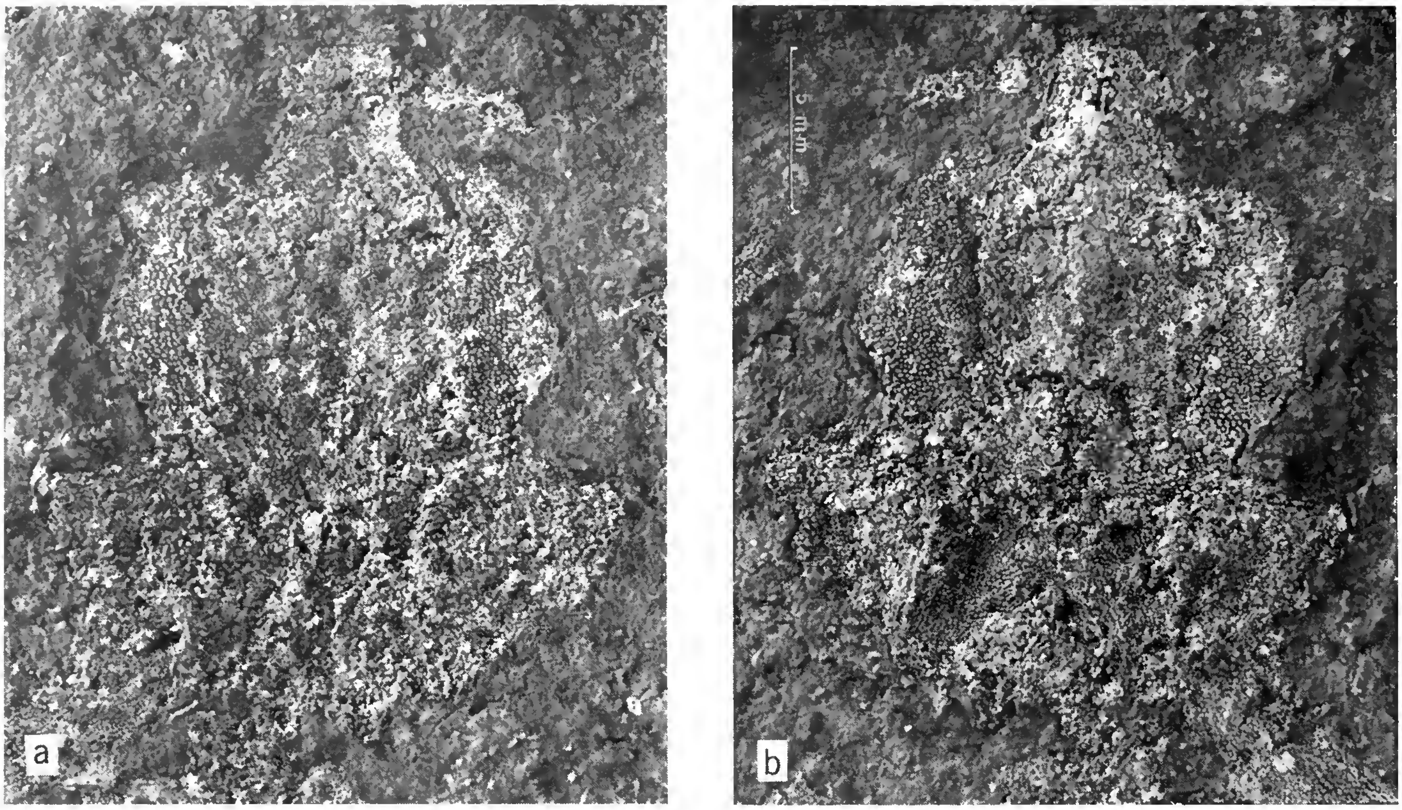

FIG. 33. Photographs of braincase (a, plate and b, counterplate) of *Promexyele peyeri*, PF6578.

should be able to recognize at least a certain resemblance of these structures to the differentiation of modern chondrichthyan brains. A recognizable resemblance does indeed exist to the dorsal side of the *Rhinochimaera pacifica* brain as illustrated by Garman (1904, pl. 14, fig. 3). From front to back one would recognize depressions for the telencephalon (anterior widening of the median depression), an elongated diencephalon region, (proper in length, but much wider than the diencephalon of *Rhinochimaera* would require), the mesencephalon and metencephalon complex followed by the medulla channel.

The relief on the counterplate consists, near the posterior end, of a sagittal, narrow ridge, flanked by broad valleys that seem to unite in front of the ridge. There are also fairly pronounced, longitudinal lines of demarcation medial to the bulbous orbital regions as well as a large number of smaller features of the relief, that may or may not have morphological significance. We are unable to relate this pattern to the ventral aspect of the brain of any chondrichthyan, which renders the interpretation of the plate, as reflecting the dorsal aspect of the brain, doubtful.

The dentition consists of a large number of tricusped teeth consisting of a main crown cusp and two side cusplets which, probably depending upon their position in the dentition, are nearly of the same size or differ considerably in size (fig. 34). The bases of these teeth are slightly expanded beyond the crowns and are characteristically rough on the underside (fig. 34). We assume that these teeth stood in labio-lingual rows (tooth families) on the jaws in typical shark fashion (fig. 35). Several teeth in each row were probably functional at the same time. Symphyseal tooth rows are apparently present, but in none of the specimens are they preserved in situ: in the type specimen (PF5911) there are three differently shaped teeth located in a row which might be symphyseal teeth. These teeth are single-cusped, except for the middle one which bears one minute side cusplet. An idea as to how the dentition may have looked is given in Figure 35.

In contrast to *Iniopteryx*, the mouth cavity of *Promexyele* was partially covered with denticles that fused basally to form a number of tooth-studded plates (fig. 34) of different shape and size (not unlike those of *Sibyrhynchus denisoni*, see below). There is at present no specimen that shows these plates sufficiently complete and in place to permit their designation as elements of the floor or the roof of the mouth cavity. Tentative identification, however, can be achieved by comparison with similar elements in *Sibyrhynchus* (fig. 47). PF2358 does show the plates in the area of the mouth cavity and an array of cartilage rays that probably supported the opercular flap (fig. 36).

The shoulder girdle elements are best seen in PF2916, PF2358, and CL153. These are long cartilage bands curved around the posterior end of the skull and reaching a considerable distance forward on the ventral side (fig. 36). The articulation with the basal elements of the pectoral fins is far dorsal on these elements, pos-

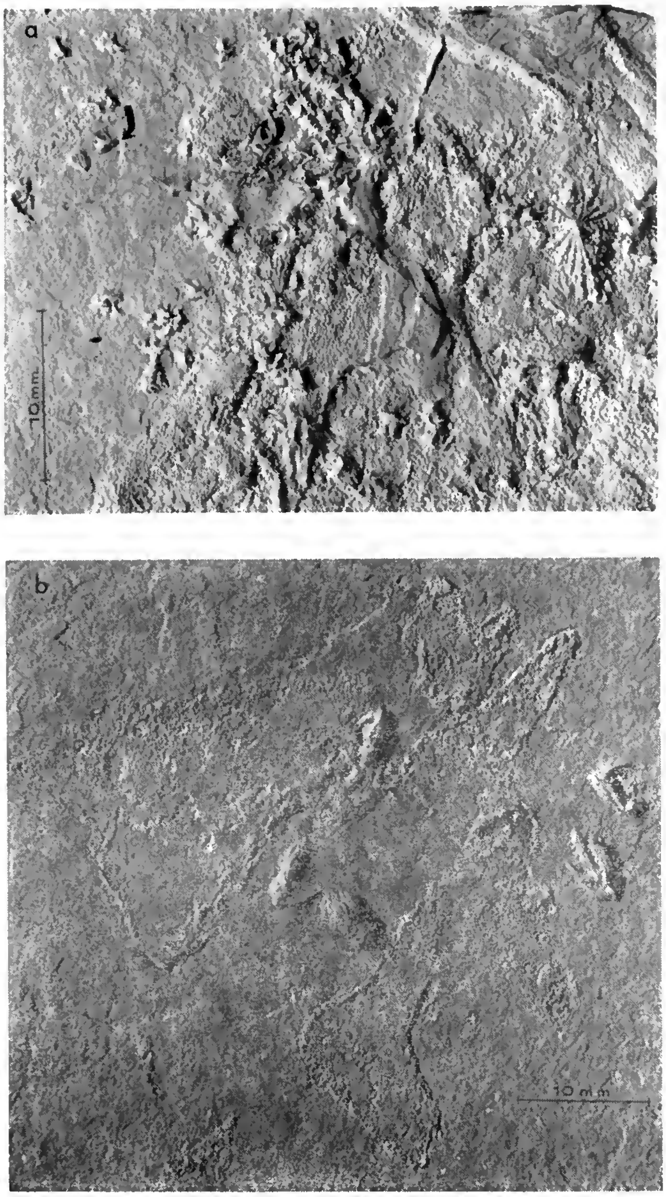

FIG. 34. *Promexyele peyeri*, PF5911 (holotype). **a**, scattered dentition teeth (arrows) showing the tricuspid character and, **b**, a portion of the pelvic area showing the pelvic cartilages, one of the basipterygia, two tenacular cartilages, and a scattering of tenacular hooks.

sibly somewhat higher than in *Iniopteryx*. The exact shape of the basal element of the pectoral fin cannot be determined; it is certainly much smaller (shorter) than in *Iniopteryx*. The first (anteriormost) fin ray is barely enlarged in PF2358, surely a female. The number of finrays in this specimen is six, including the first ray (fig. 36). In males such as the type specimen, the first ray is much thicker than the other rays and it was evidently covered with hooks that gave it the appearance of a rough rasp. The hooks decrease in size to the distal end where they are minute. These rasp hooks differ from those in *Iniopteryx* in that they have much more expanded bases (fig. 37)—little platforms that paved much (or all) of the cartilage surface of the ray, each bearing a recurved denticle. As in *Iniopteryx*, the rasp hooks are modified dermal denticles consisting of a thick coat of orthodentine, in the crown region probably covered by vitrodentine, and an undivided pulp cavity. In CL153 there are enlarged first finrays but not a trace of rasp hooks and the specimen was thus identified as a female; the generally good state of preservation of the available parts of the skeleton makes it unlikely that the rasp hooks were lost during bacterial degradation of the carcass. Considering the otherwise notable individual variation in these animals it is likely that the first pectoral finray in some female individuals reached the same size as that of males.

The pelvic apparatus, although disarticulated, is best seen in the type specimen (fig. 31) and the reconstruction (fig. 38) is one of several possibilities to be verified by future articulated remains. As presently interpreted, the vaguely boomerang-shaped pieces seem to be the pelvic cartilages; the large triangular cartilages are no doubt the basipterygia (to judge by the shape of these elements in *Iniopteryx*). There are two additional triangular elements (fig. 31). The smaller element might be one of a pair of cartilaginous bases for the three tenacular double hooks. The larger might be its mate, asymmetrically developed, or it might be a sagittal cartilage plate associated with the dorsal fin; the latter appears to us to be more probable.

The clasper mechanism (fig. 31 and reconstruction, fig. 38) consists on each side of a series of five short cartilage pieces that have two parallel straight sides and a convex and a concave outline at present. In life these elements probably were circular in cross-section which is the reason why we have reconstructed them with their flat sides in articulation (fig. 38). These short elements are followed by a pair of much elongated rods that taper to a fairly sharp posterior end. Near their tips there is an accumulation of tiny denticles that probably are the clasper hooks (fig. 39). These are faintly curved needle-shaped denticles.

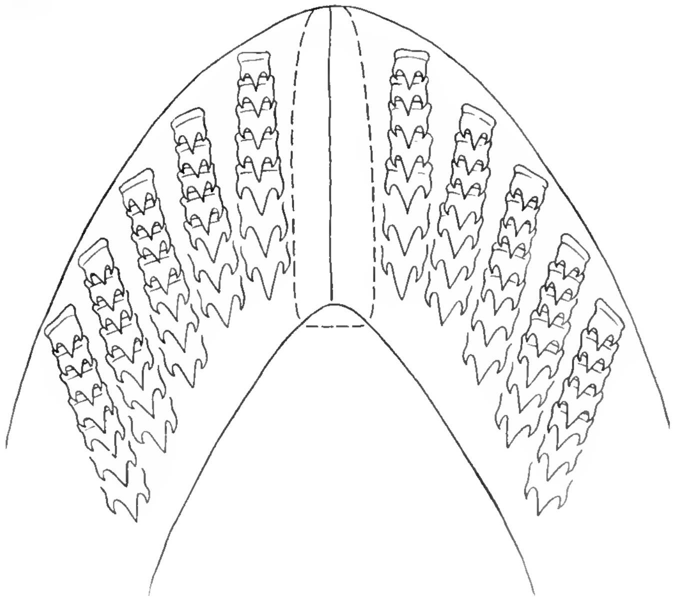

FIG. 35. Present interpretation of the dentition of the lower jaws of *Promexyele peyeri*.

FIG. 36. Radiograph of a female specimen of *Promexyele peyeri*, showing both pectoral fins (arising from the nape of the neck) without fin rasps; both scapulocoracoids *in situ;* the hyoid rays supporting the opercular flap and the presence of mouth plates whose detailed shapes, however, cannot be made out. Below the pectoral fins, part of the vertebral column is seen. Specimen PF2358.

Appearance in life.—The reconstruction attempted in Figure 38 assumes that the overall habitus of the species was similar to that of *Iniopteryx*. This seems justified in the sense that the vertebral column, dorsal and tail fins, to the extent that they are preserved, show no difference from the compared genus.

Locomotion.—The structure of the pectoral fins is sufficiently different from *Iniopteryx* to suggest a somewhat different effect from a basically similar use of the fins. It seems probable that *Promexyele peyeri* like *Iniopteryx rushlaui* propelled itself by vertical motions of the pectoral fins. In this case, however, there are no broad attachment surfaces for the fin musculature and the fin surface is supported mostly by long, thin cartilage rods. These parameters suggest that the fins were highly flexible and the vertical motions were relatively slow and were lacking power in the downstroke. *Promexyele peyeri* thus was most likely a slow-moving fish that may have had a rather restricted home range.

Sex ratio.—The total number of specimens that can be sexed is rather small (8), and, assuming that our identification is correct, there are as many females as there are males.

Geographic and stratigraphic distribution.—*Promexyele peyeri* is not particularly common in any of the localities tested, and by far most of the specimens come from the eastern fringes of the Illinois Basin in Indiana. In the younger shales (Westphalian upper D) of the western part of the Forest City basin, this species appears to be as rare as *Iniopteryx* is in Indiana.

FIG. 37. Photograph of pectoral rasps of *Promexyele peyeri*, PF5911 (holotype), showing the large numbers of rasp hooks diminishing in size distad.

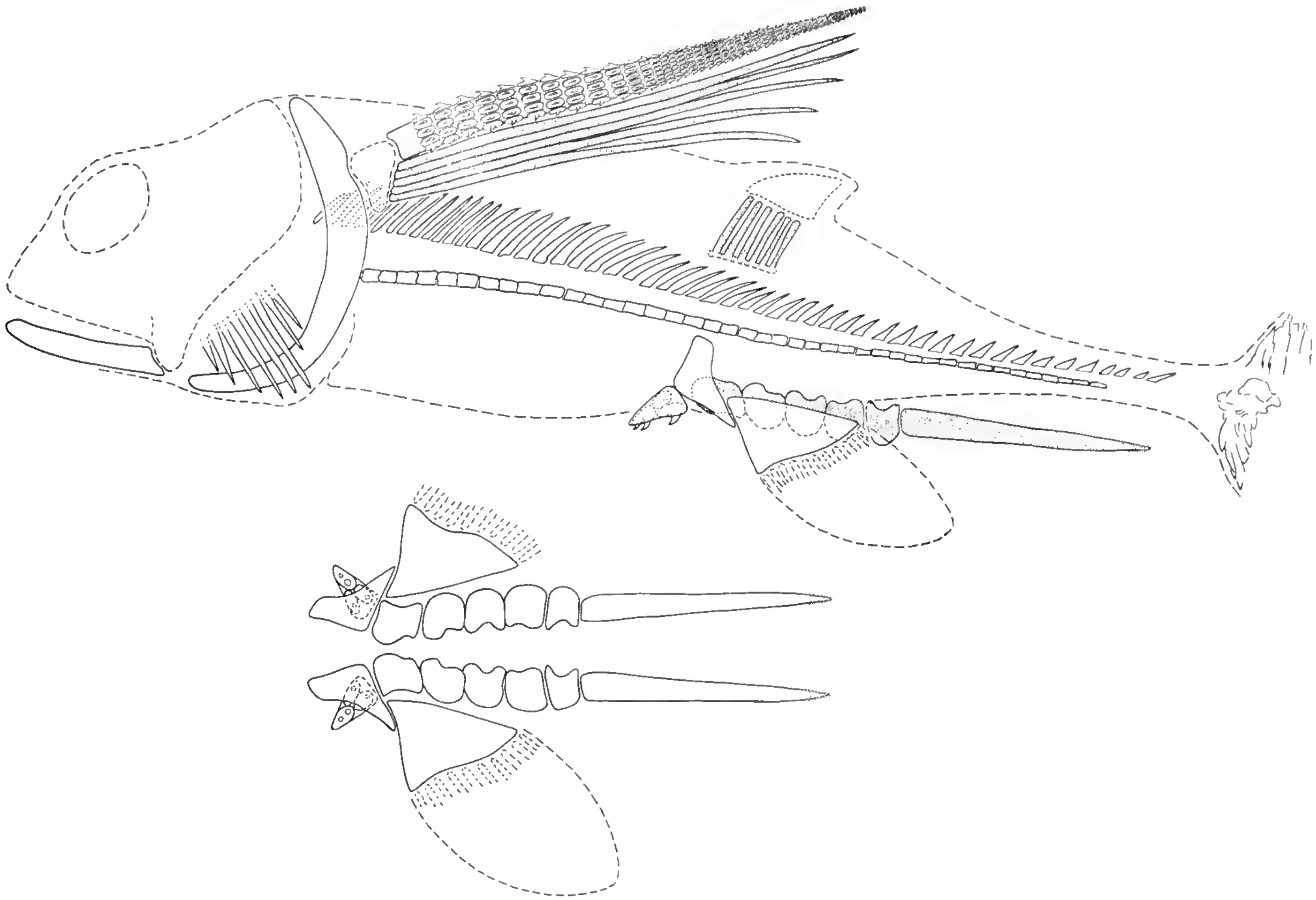

FIG. 38. Tentative reconstruction of the skeleton of *Promexyele peyeri* in side view. The proportions of the various parts are only approximately correct. Below is a ventral view of the pelvic complex of the male.

FIG. 39. Photograph of clasper hooks near distal ends of clasper elements of *Promexyele peyeri*, PF5911.

Promexyele bairdi,[1] n. sp.

Type.—PF6710, ♂, a large part of a skeleton, lacking the tail region.

Horizon and locality.—Wea Shale, Westerville formation, Kansas City group, Westphalian D., Pennsylvanian. Papillion, Nebraska.

Referred specimens.—

WEA SHALE

PAPILLION

PF7203, ♂, partial skeleton, showing the pectoral rasp and much of the clasper mechanism, (W. D. White)

PF7200, ♂, skull and shoulder, good pectoral fin, (W. D. White)

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[1] Named for Dr. Donald Baird of Princeton University, who has a deep interest in Pennsylvanian faunas, and who has consistently given us the benefit of his background and experience.

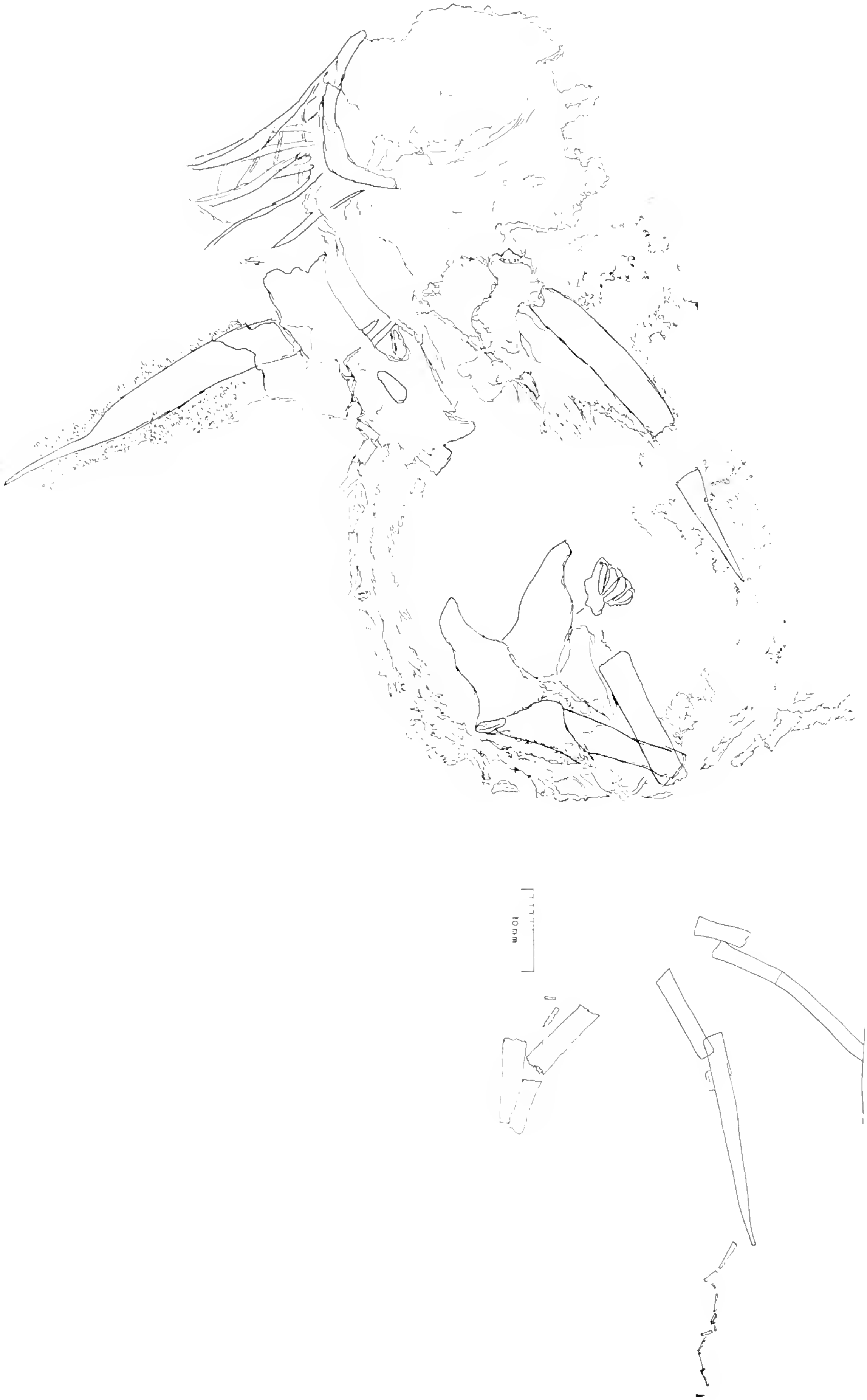

FIG. 40. Camera lucida drawing of *Promexyele bairdi*, PF6710 (holotype) (see also fig. 43).

FIG. 41. Camera lucida drawing of the pectoral fin of *Promexyele bairdi*, PF7200. Note the abrupt reduction in diameter of the rasp and the presence of small and large rasphooks near the proximal end of the rasp.

PF7243, ♂, partial, articulated specimen, (W. D. White)

EXCELLO SHALE

BARRET CEMETERY

PF6455, ♂, disarticulated skeleton of juvenile individual, XR: Barret No. 11

Characterization.—First fin rays of pectoral fins enlarged, but not as much elongated as in *P. peyeri*, covered with a large number of hook-shaped denticles with relatively small bases (probably in excess of 150 per rasp). Sharp reduction in diameter of rasp in distal third of its length. Two or three tenacular hooks (?double) on either side. Clasper apparatus extraordinarily elongated, consisting of at least four much elongated pieces of cartilage on each side, the terminal one being extremely slender. No clasper hooks at the distal end.

Description.—The type specimen (fig. 40) shows the characteristic features of this fish very well, but adds little to the knowledge of the genus. The skull is notably disturbed. No teeth or mouth plates are visible and the cartilages of the head region look delicate —all features that characterize many specimens of *Promexyele peyeri*. The head region shows the cartilage supports of the opercular flap and some elements that probably belong to the hyobranchial apparatus (fig. 40).

Shoulder girdle and pectoral fins are much disturbed except for the pectoral rasps, which show a peculiarity not seen in any other iniopterygians, namely, a sudden reduction in the diameter of the cartilage rods in the distal third of the rasps (fig. 40). Since this feature is also present in the referred specimen PF7200 (fig. 41), we assume that it characterizes the species. The rasps are covered with a large number of hooks (probably more than 150 per rasp) all of which are relatively small, even at the proximal ends of the rasps. These denticles have relatively small bases and thus differ notably in shape from those of *P. peyeri*. Since there are denticles of different sizes both in the proximal areas of the rasps as well as in the distal parts, it is possible that there are specially differentiated rows of slightly larger denticles, for example, along the anterior edges of the rasps. In addition to the rasp, there are 12 slender rays in the pectoral fin of PF7200, seven of which are short and stand at an angle to the long ones, thus perhaps forming the supports for an aileron, as in *Iniopteryx rushlaui*.

The pelvic area is remarkable. The region is slightly disturbed in the type specimen so that the exact extent of the pelvic elements and the basipterygia (fig. 40) cannot be determined with accuracy. If our interpretation of the pelvic complex is correct (fig. 42), it would suggest that the pelvic cartilages are relatively much larger than

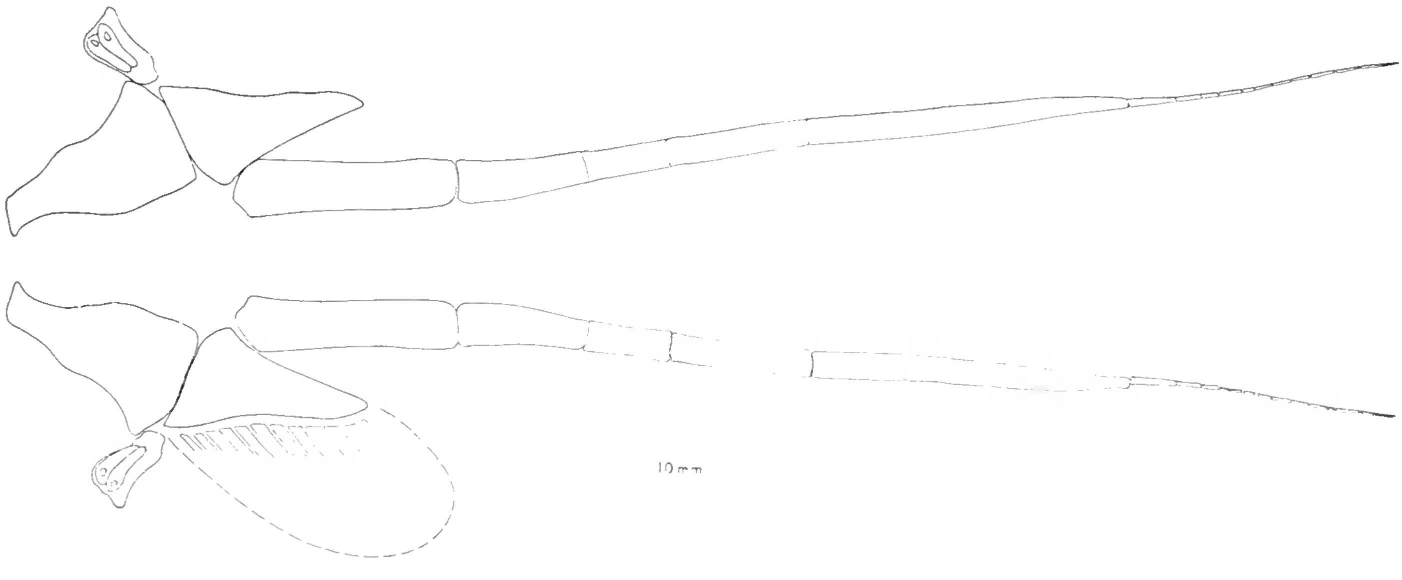

FIG. 42. Reconstruction of the pelvic complex of the male of *Promexyele bairdi*, based on several specimens; see also fig. 43.

FIG. 43. Photograph of *Promexyele bairdi*, PF6710 (holotype).

in other iniopterygians, while the basipterygia are relatively smaller. The uncertainty is due to the fact that these elements appear to overlap to an undeterminable amount. Off to one side of this complex is a much smaller piece of cartilage (or, more likely, two, that partially overlap) bearing at least five tenacular hooks that may or may not be double hooks. Another such hook is located at the presumed junction of one of the pelvic and basipterygial elements (fig. 40).

The claspers are extremely elongated and end in a thin whip (figs. 42, 43). It is difficult to determine how many pieces of cartilage contribute to each clasper, but we believe them to be at least four. Apparently there are no clasper hooks at the end of the whip.

Family **Sibyrhynchidae**, nov.

Characterization.—Iniopterygia in which the labiolingual tooth rows (tooth families) are basally fused to form tooth whorls of different size and shape. Meckel's cartilages are fused at the symphysis.

Genera.—Sibyrhynchus, Iniopera, Inioxyele.

Genus **Sibyrhynchus**,[1] gen. nov.

Characterization.—Iniopterygians with sharp-toothed dentition consisting of 12 pairs of different tooth whorls; "canine" whorl fifth from symphysis in the upper jaw, third from symphyseal whorl in lower jaw. Snout armored with three tubercles, a blunt median one flanked by two stout tubercles; a large, sharp-pointed tubercle projects from the anterior end of the lower jaw. Denticulate roof and floor plates of the mouth cavity irregular in outline; the denticles tending to fuse basally in linear rods that form stellate complexes, (ca. 5 on either side of the palate). Multiple tenacular hooks located on basipterygium. Claspers consisting each of a stout proximal cartilage rod, followed by a series (ca. 6) of short pieces and terminating in an elongated, distally blunt rod.

Type species.—Sibyrhynchus denisoni, n. sp.

Sibyrhynchus denisoni[2], n. sp.

Type.—FMNH PF6408, slightly disturbed ♂ skeleton, lacking the tail. XR: Bethel No. 56.

Horizon and locality.—Black, sheety shale over coal IV-A (Excello shale equivalent), Petersburg formation, Westphalian D, Pennsylvanian; stripmine headwall, about center of NW ¼ Sec. 3, T3S, R7W (Augusta Quadrangle), about ¼ mile SE of Bethel Church, Pike County, Indiana.

Referred specimens.—

QUEEN HILL SHALE

PLATTSMOUTH

PF7216, —, scatter of hardparts, (M. Eisele)

PF7224, —, scatter of hardparts, (G. R. Case)

EXCELLO SHALE

BETHEL CHURCH

PF6504, —, chewed skull, XR: Bethel No. 21

PF6506, ♂, clasper apparatus and partial tail fin. XR: Bethel No. 20

PF6514, —, chewed skull. XR: Bethel No. 26

PF6515, —, gastric residue including tubercles and tooth whorls of *Sibyrhynchus.* XR: Bethel No. 29

PF6525, —, gastric residue of very small individual. XR: Bethel No. 32

PF6559, —, gastric residue, containing two specimens of different size. XR: Bethel No. 43

PF6576, —, mutiliated skull

PF6615, ♂, large portion of articulated skeleton with good vertebral column and pelvic area. XR: Bethel No. 53

PF6616, —, chewed remains of skull. XR: Bethel No. 54

PP6617, —, gastric residue, containing identifiable hard structures of *Sibyrhynchus.* XR: Bethel No. 52

BARRET CEMETERY

PF6565, —, gastric residue mass, containing hard parts of this species. XR: Barret No. 17

BEAVER POND

PF6463, —, gastric residue mass, containing hard parts of this species. XR: Beaver No. 1

PF6582, —, gastric residue mass, containing hard parts of this species. XR: Beaver No. 3

PIT 12

PF6729, —, gastric residue mass containing hard parts of this species. XR: C.P.L. No. 13

PIT 14

PF6537, —, gastric residue pellet, containing hard parts of this species. XR: Pit 14, No. 8

PF6538, —, gastric residue mass, containing hard parts of this species. XR: Pit 14, No. 9

PF6539, —, partial skull. XR: Pit 14, No. 7

MECCA QUARRY SHALE

MECCA QUARRY

PF2806, ♀, partial skeleton, partly articulated. Mecca quarry level B4.1; XR: MQ No. 12

PF2819, —, mutilated skull of fairly large individual. Mecca quarry, level B1.2; XR: MQ No. 226

PF2835, —, gastric residue spatter of hard parts of this species. Mecca quarry, level B3.3; XR: MQ No. 151

PF2900, —, scatter of hard parts of this species. Mecca quarry, level B1.1; XR: MQ No. 76

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[1] From *sibyne*=hunting spear, and *rhynchos*=snout.

[2] Named for a friend and colleague, Dr. Robert Denison, former Curator of Fossil Fishes, Field Museum of Natural History.

PF2915, —, gastric residue pellet containing hard parts of this species. Mecca quarry, level A1.1; XR: MQ No. 167

PF2918, —, gastric residue with hard parts of this species. Mecca quarry, level B4.2; XR: MQ No. 119

PF2920, ♂, mutilated, partial skeleton. Mecca quarry level B4.2; XR: MQ No. 66

PF2936, —, gastric residue mass, containing hard parts of this species. Mecca quarry, level B1.1; XR: MQ Nos. 217, 91

PF3013, —, gastric residue spatter containing hard parts of this species. Mecca quarry, level B1.4; XR: MQ No. 228

PF6716, —, gastric residue mass containing hard parts of this species. Mecca quarry, level B2.4

PF6747, —, gastric residue, containing hard parts of this species. Mecca quarry, level B1.1; XR: MQ No. 211

PF6760, —, gastric residue mass containing hard parts of this species. Mecca quarry, level B3.2

PF6764, —, gastric residue pellet. Mecca quarry, level B1.4; XR: MQ No. 212

PF2940, —, scattered skeleton, Mecca quarry, level B1.1; XR: MQ No. 217, 91

U.S. Highway 41

PF1019, —, scattered remains. XR: DS No. 16

PF1034, —, scattered remains, excellent detail

PF1036, ♂, small articulated skeleton with skull missing

Mine Creek

PF6762, —, isolated hard parts

Montgomery Creek

PF6623, —, gastric residue mass, containing hard parts of this species. XR: Montgomery No. 2

West Montezuma

PF6634, ♂, good partial skeleton. XR: Montezuma No. 4

PF6635, —, slightly mutilated skull. XR: Montezuma No. 9

PF6637, ♂, gastric residue containing hard parts of this species

PF6639, ♂, part of a fair-sized specimen without skull. XR: Montezuma No. 18

PF6641, —, disarticulated, large specimen

Moorehead's Bank

PF6650, —, part of a skull with anterior tooth whorls of lower jaw and tubercle in place. Collected and donated by Mr. John Carlson

Chinook Mine

PF5879, —, gastric residue mass containing hard parts of this species. XR: Chinook No. 3

Logan Quarry Shale

Logan Quarry

PF2351, ♂, gastric residue pellet. Logan quarry, level G; XR: LQ No. 301A

PF2354, —, part of a skull, incompletely recovered. Logan quarry, level G; XR: LQ No. 237

PF2355, —, mutilated skull and shoulder region. Logan quarry, level G; XR: LQ No. 194

PF2363, —, mutilated skull. Logan quarry, level J; XR: MQ No. 137

PF2365, —, gastric residue pellet, containing hard parts of this species. Logan quarry, level J; XR: LQ No. 37

PF2592, —, gastric residue, containing hard parts of this species. Logan quarry, level G; XR: LQ No. 282

PF2594, —, part of a skull with excellent dentition. Logan quarry, level G; XR: LQ No. 303

PF2632, ♂, disarticulated, but excellent specimen; good braincase, lower jaw. Logan quarry, level J; XR: LQ No. 263

PF6730, —, gastric residue mass containing hardparts of this species. Logan quarry, level F

PF6757, —, scatter of *Sibyrhynchus* parts. Logan quarry, level J; XR: LQ No. 124

Hajji Hollow

PF5894, —, mutilated skull. XR: Hajji Hollow No. 3

Characterization.—Same as for genus.

Description.—*Sibyrhynchus denisoni* is probably the largest of the presently known iniopterygians, but none of the specimens on hand permit a length measurement of the entire fish. This species is also easily identified, even in gastric residues, because of the relatively large size of the tooth whorls, the snout tubercles, especially the median upper one which has a characteristic apperance, the large tubercle on the lower jaw, and the spidery tooth plates in the roof and on the floor of the mouth cavity. The latter, however, may be confused with similar plates in *Promexyele.* The reconstruction (fig. 56) is based on several specimens (mostly PF6408, PF6506, PF6615) that are not the same size, hence we cannot be absolutely certain that the proportions of the various parts of the skeleton are correct, though the size factor was taken into account. There are other uncertainties: in none of the presently available specimens is there definite evidence of a dorsal fin, and the precise morphology of the pectoral fin is not determinable at this time.

Skull:

An excellent neurocranium and disarticulated lower jaw are preserved in PF2632 (fig. 44) and a somewhat less perfectly preserved skull belongs to PF6634. In both cases the neurocranium is seen in dorso-ventral position on radiographs. Figure 44 was rendered from a pair of much enlarged stereo X-ray pictures according

FIG. 44. *Sibyrhynchus denisoni*, PF2632, skull complex drawn from enlarged stereo radiographs. The neurocranium is preserved in dorso-ventral position and is seen from the ventral side.

to the technique described earlier (Zangerl, 1966). The neurocranium, seen from the ventral side in Figure 44, shows very clearly the articular facettes for the lower jaw; they are part of a ventro-lateral cartilage mass that is attached, at the postero-lateral corners of the neurocranium, to a dorsal cartilage mass. A ventral plate of cartilage, furthermore, extends from the articular facettes forward toward the blunt snout. Below the facettes the ventral cartilage mass shows a transversal ridge on either side of a median plate which extends to the occiput. The posterior margin of the dorsal cartilage mass shows three pairs of symmetrical projections. On the X-ray picture there is no evidence of an otic capsule or inner ear structures, the orbits, the nasal capsules or the outline of the brain enclosure.

The reason for this lack of detail, while the overall structure is readily recognizable as a neurocranium, is the mode of preservation of the three dimensional organ, whose external and internal surfaces were supported only by single layers of calcified cartilage prisms held together by connective tissue. Following death the head decomposed by bacterial action in an absolutely quiet, completely undisturbed burial environment. In the course of this process the cranium settled gradually into an essentially two dimensional state with every part of the originally vaulted structure being projected vertically into the fossil plane. This had, of course, the consequence that all curved surfaces and those not parallel to the fossil plane, became reduced in area, which resulted in wrinkling of the surfaces and more often in the local jumbling of calcified cartilage prisms.

One feature of the skull however, is unmistakable: the fact that the palatoquadrates are fused to the neurocranium in such manner that it is completely impossible to surmise the original boundaries of these elements. The jaw suspension is thus autostylic, as in chimaeroids. The lower jaw consists of symphyseally fused Meckel's cartilages; the rami stand at an angle of about 35–40° in

PF2632, PF6634, PF6757. This means that the articular facettes are closer together in the lower jaw than in the neurocranium of PF2632 and we have assumed that during decomposition of the neurocranium the articular facettes underwent a slight lateral displacement. In Figure 45b, the dotted lines indicate the preserved condition, the solid line our correction to fit the posterior width of the mandible.

HYOBRANCHIAL APPARATUS

The hyobranchial apparatus of *Sibyrhynchus* consists, as far as one can presently determine, of a characteristic, six-sided cartilage plate whose anterior and posterior sides are joint facettes and the element shows consistently symmetrically placed foramina (fig. 46). In addition, there is a smaller piece, (also provided with articular facettes and either a deep central pit or a large foramen), a pair of elongated elements with joint facettes on one end, and a blade-like flare on the other (fig. 46); matching almost perfectly the ceratohyals (ceratohyals plus possibly hypohyals, Nelson, 1969) figured for *Callorhynchus smythi* by Garman (1904, pl. 13-3). The element with the paired foramina is perhaps the first basibranchial and in front of it there was probably a glossohyal, not yet seen in this species, but commonly noted in *Iniopera* (see below), and almost certainly present in *Sibyrhynchus* in light of the anterior articular facettes of the first basibranchial.

In *Sibyrhynchus denisoni* the snout is armored with three strong tubercles consisting mostly of trabecular dentine. The medial, blunt one, is highly characteristic on radiographs (figs. 44, 47) where both the dorsal and ventral sides of the tubercle are visible. The ventral edge is nearly straight, while from the dorsal face project a number of long radii far beyond the ventral edge (fig. 45a, b). This element is flanked by two more or less perfectly conical tubercles, also provided with radii on their dorsal sides and straight edges ventrally (fig. 45a, b). The tip of the lower jaw is provided with a much larger, sharply pointed tubercle whose dorsal rim is straight, while its ventral side projects into several very long radii over the ventral side of the mandible, (figs. 44, 45c, d, 47). In Figure 45 we have, furthermore, attempted to show the dentition of both upper and lower jaws, the elongated structures representing tooth whorls, and the spidery dental plates of the roof and floor of the mouth cavity.

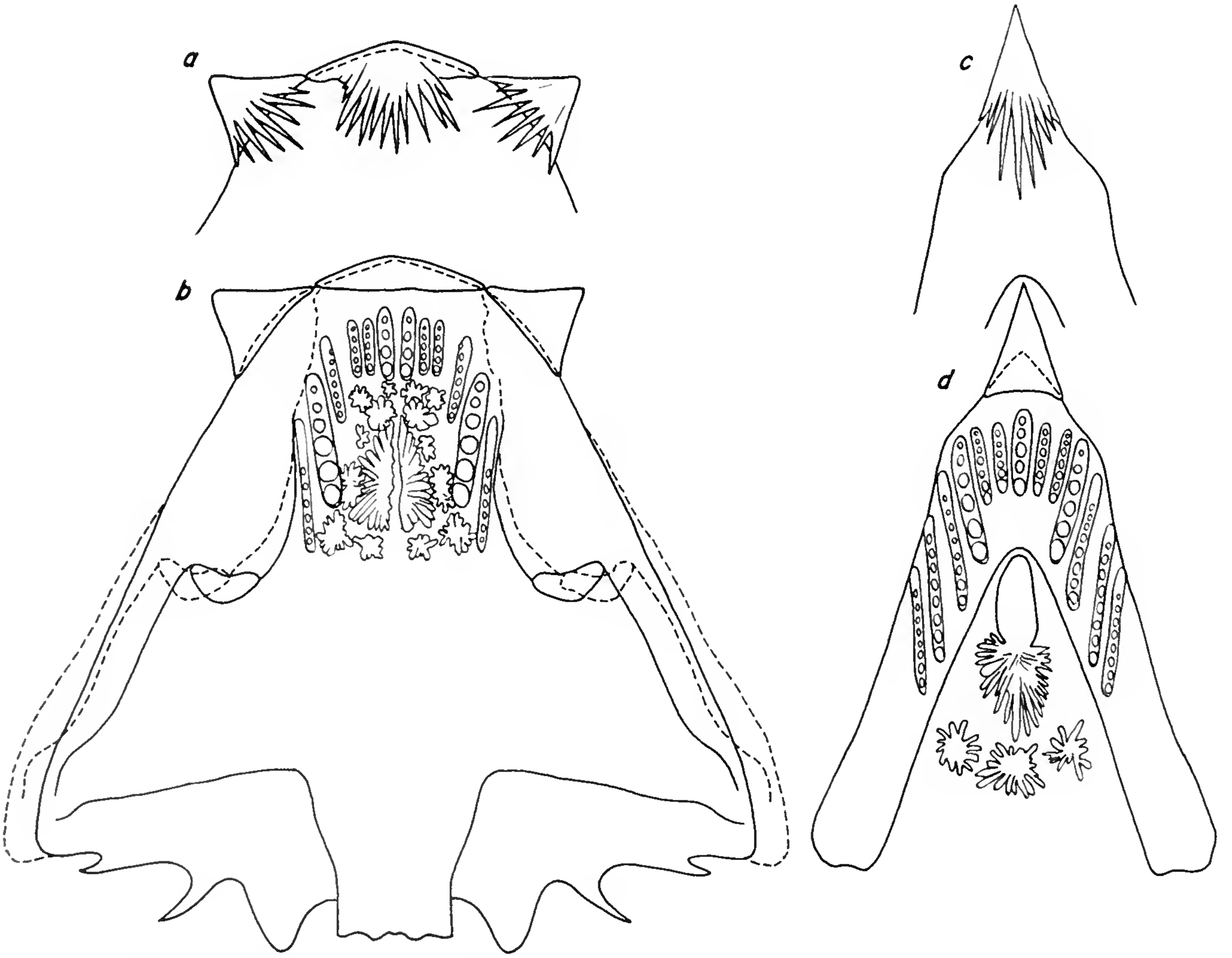

FIG. 45. *Sibyrhynchus denisoni* neurocranium and lower jaw with snout tubercles, tooth whorls, and mouth plates. Dotted line is outline of neurocranium as preserved (PF2632, fig. 44); solid line is width of neurocranium adjusted to width of mandible. **a**, snout tubercles from dorsal view; **b**, snout tubercles, dentition, and palatal plates seen from ventral view (tooth whorls schematized); **c**, tubercle on lower jaw from ventral view; **d**, tubercle, dentition, and floor plates of the mouth cavity as seen from dorsal view.

DENTITION

The dentition of *Sibyrhynchus* (and the genera *Iniopera* and *Inioxyele*, see below) is most remarkable, indeed. In *Sibyrhynchus* it consists of six pairs of tooth whorls in the upper jaw, and six pairs of whorls plus an unpaired symphyseal one in the lower (figs. 45b, d). Each pair of tooth whorls differs from all others in the shape of the whole structure, and the size and number of teeth. Thus *Sibyrhynchus* displays a degree of dental diversity not realized in any other fishes, and rivals or even exceeds the heterodonty of the mammalian dentition.

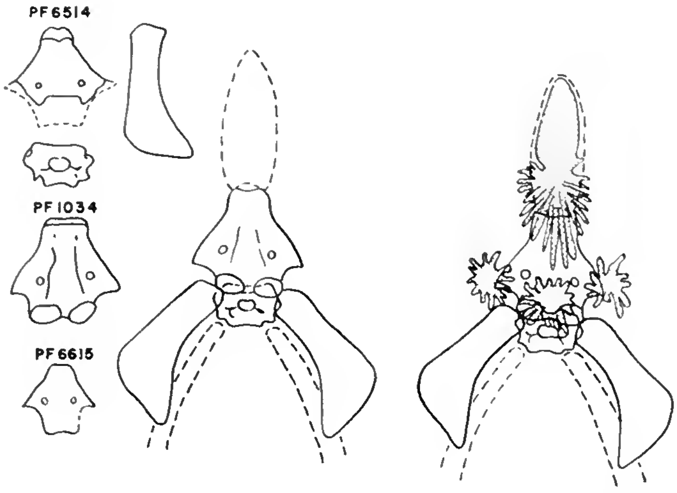

FIG. 46. Hyobranchial elements of *Sibyrhynchus denisoni* with the possible mode of superposition of the denticulated plates on the floor of the mouth cavity. Scale: x 0.75.

Each tooth whorl consists of a number of teeth, belonging to a labiolingual row, called "tooth family" in sharks, whose bases have fused so that the entire tooth family has become a tooth whorl in which the individual tooth crowns are separated from one another and clearly distinguishable from the base (fig. 48a). The enlarged base of each whorl consists of lateral sheets of dentine that enclose one large space into which open the pulp cavities of the component teeth (fig. 48b). In life this space was not a cavity. Instead, it was filled with calcified cartilage, a pronounced ridge on the neurocranium or the mandible that formed the seat of the tooth whorl (fig. 48b).

In sharks the state of development of the teeth of a tooth family decreases from the functional tooth on the edge of the jaw to the anlagen stages at the lingual end of the dental lamina (see, for example, Peyer, 1968, pls. 7a, 8b, 9b). In the early stages of hard substance deposition, the teeth contain very large pulp cavities enclosed by thin walls of orthodentine covered by vitrodentine; in the fully mature teeth the pulp cavities are reduced in volume and the tooth walls have correspondingly increased in thickness. Precisely the same mode of tooth differentiation is seen in an iniopterygian tooth whorl; at the lingual end of the whorl the teeth are thin-walled and enclose large pulp cavities, a clear indication that this end was near the end of the dental lamina. One can safely assume that in life younger tooth stages preceeded the most immature teeth on the fossil whorls and that these were not preservable. Reflecting the growth of the animal as a whole the teeth show a distinct size increase toward the immature end of the whorl (fig. 48a). In contrast to the condition in sharks, however, there is no evidence in the tooth whorls that the earliest teeth were shed after a certain period of function. On the contrary, many whorls show teeth only on the middle and posterior (lingual) parts, the anterior (labial and oldest) regions being devoid of them. It seems probable that the small teeth there have worn off during the life time of the individual.

In none of the specimens is the entire dentition perfectly in place; in fact, instances where numbers of tooth whorls are seen in place are rare exceptions. In most specimens the whorls are more or less out of place and elements of the upper and lower dentitions tend to be mixed together, or only a part of the dentition is present or visible. Because of these considerable difficulties it is not yet possible to describe in detail the morphology of

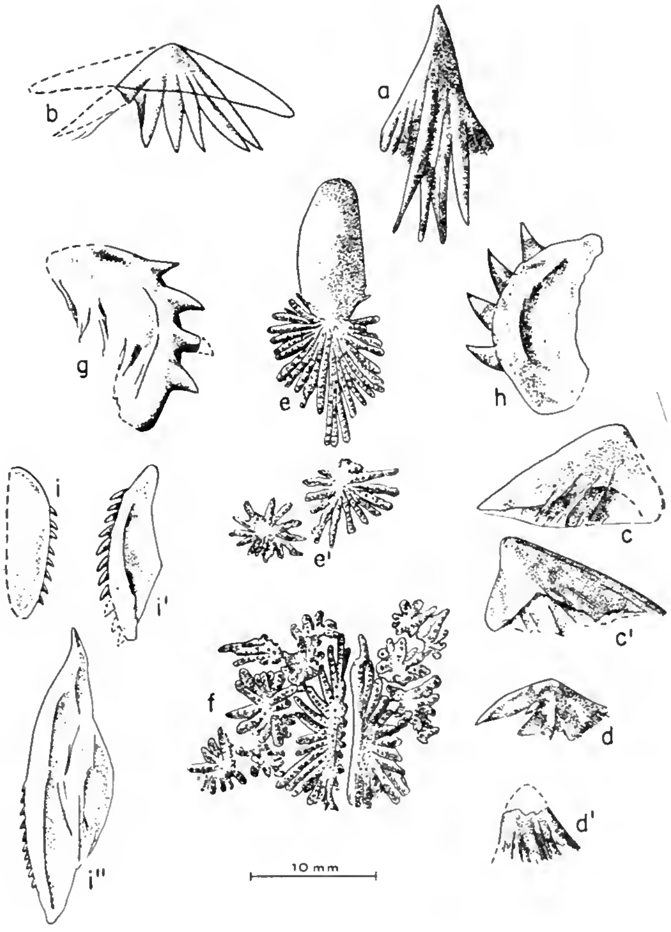

FIG. 47. Drawing of snout tubercles, tooth whorls, and tuberculated plates of the mouth cavity of *Sibyrhynchus denisoni*, PF6408 (holotype), made from enlarged stereo radiographs and what can be seen on the specimen. **a**, median tubercle on lower jaw; **b**, median tubercle on snout; **c** and **c'**, lateral tubercles on snout; **d** and **d'**, additional tubercles about the head; **e** and **e'**, denticulated plates on the floor of the mouth cavity; **f**, denticulated plates on the roof of the mouth cavity; **g** and **h**, "canine" tooth whorls; **i**, **i'** and **i"**, lateral tooth whorls of upper and/or lower jaw.

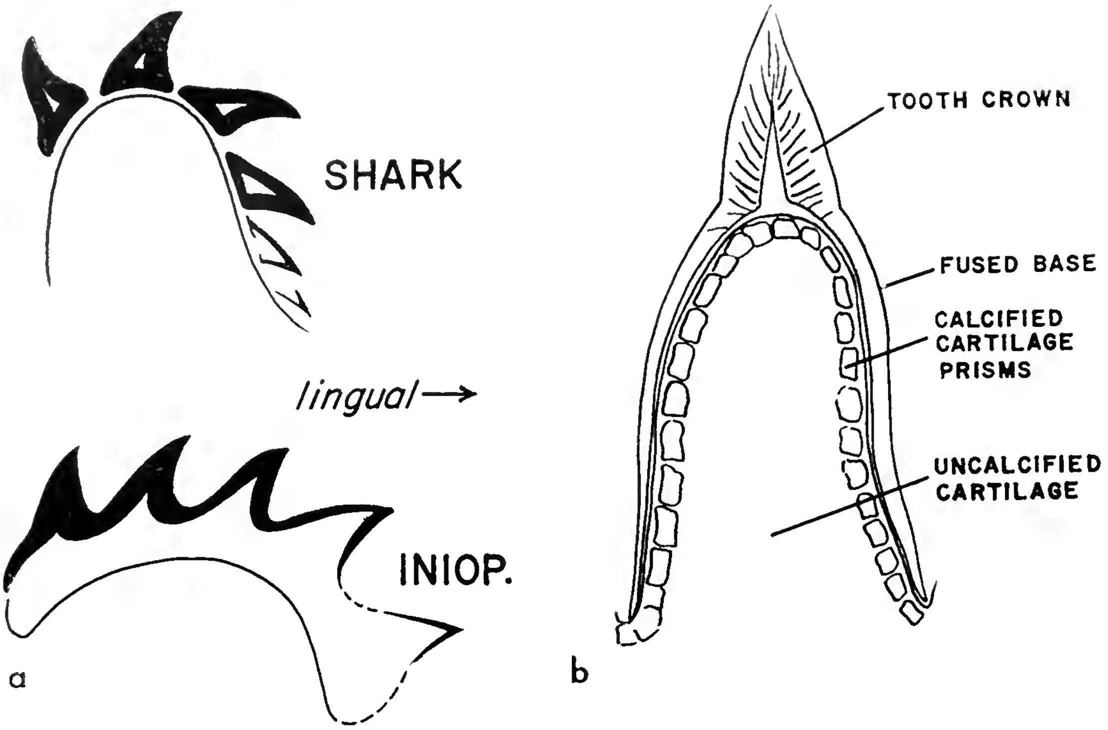

Fig. 48. **a**, Diagrammatic section across the jaw of a shark showing the teeth and tooth anlagen along the dental lamina, with the youngest anlagen at the lingual end of the lamina. Below, a section through a tooth whorl of an iniopterygian such as *Sibyrhynchus*, showing the basic similarity to the shark condition; the teeth are fused at their bases, but the ones at the lingual end of the whorl are clearly younger teeth than those at the labial end. **b**, Section through an iniopterygian tooth whorl at a right angle to that shown in *a*. It shows that whorl riding on a ridge of cartilage with calcified prisms just beneath the perichondrial membrane (not preserved in the fossils). The tooth crown consists of orthodentine surrounding a pulp cavity that diminishes in volume with the age of the tooth crown.

all classes of tooth whorls, and such identifications as we have made are tentative.

The description of the tooth whorls requires a terminology, and we shall label them from the symphysis outward and backward in series P-1 (for palatoquadrate-1) to P-6 in the upper jaw, M-1 to M-6 in the mandible which also has an M-s, a symphyseal whorl.

Upper and lower tooth whorls apparently differ from one another in the degree of curvature: the lower ones, especially those along the cheek, being flatter than the upper whorls. In each jaw there is a pair of whorls with large teeth. In the upper jaw it is the fifth from the symphysis, apparently in cheek position much as a carnassial tooth in a mammal; in the mandible it is the third pair, clearly in "canine" position (fig. 45).

In PF6650 part of the dentition of the lower jaw is seen *in situ* (fig. 49). The symphyseal whorl bears five teeth, the anteriormost two being broken off. The crowns are devoid of side cusplets. M-1 has seven teeth on the left element, which is better exposed. In M-2 there are eight teeth. In both M-1 and M-2 the tooth crowns have small side cusplets. The large M-3 whorls are incompletely exposed in this specimen, but their shape may be seen in PF2594 (fig. 50) where the best-exposed element shows four teeth and enough base in front and in back to have borne at least three additional teeth in life. Next to the right M-3 whorl in PF6650 there is an elongated element with a row of six teeth located on the posterior part of the whorl; a few additional teeth may have been in front of the tooth row, but the specimen does not permit a definite count. This whorl is probably M-4. Behind this whorl there is a long gap in the specimen, followed by a very much elongated whorl, probably M-6. This bears at least eight teeth and is toothless anteriorly (fig. 49). It is difficult to identify lower jaw whorls in PF2594 (fig. 50), other than the pair of M-3 that lie near the large tubercle, save for the fact that mandibular whorls are less curved than the upper ones. Thus we tentatively identified the two elements behind the large tubercle as M-4 and M-5 and the whorl with the nearly straight tooth row located between the two lateral snout tubercles as M-6. Of the upper dentition, pairs of P-1, P-2, and P-3 are in place, preserved perpendicular to the bedding of the shale and all tooth crowns have been broken off (fig. 50). This tooth complex is flanked by a pair of whorls the left one of which is seen in side view. These elements are spaced somewhat from the *in situ* complex and we have tentatively identified them as P-4, assuming that the small diastema permitted the reception of the lower "canine" whorl (M-3). Both P-4 whorls show a feature not seen in other whorls, namely the fact that the anterior teeth are not located on the ridge of the whorl, but trend over to its medial side (fig. 50). The significance of this eludes us. Next to the left P-4 there is the very much larger P-5 which bears six teeth, the last one nearly twice the size of the first. The whorl immediately in front of it has been identified as P-6 since it is rather strongly curved. It has six teeth and a large anterior area devoid of teeth.

In PF6617 a small whorl, perhaps one of the upper front tooth whorls, shows on the sides of each large tooth crown a much smaller side cusp and beneath it yet another, tiny cusplet (fig. 51).

In *Sibyrhynchus denisoni* (and apparently only in this genus) there are additional dental structures that are especially unusual in a chondrichthyan. These have been noted in the general area of the skull in the following specimens: PF2806, PF2918, PF6559, PF6582, and PF6617. The peculiar elements are teeth consisting of a shiny crown of low relief and a root (dull surface) of unmistakably mammalian character (fig. 52). Inside there is a pulp cavity and a typical root canal.

A thin section through one of these elements in PF2918 (fig. 52) shows three tissues: dentine, vitrodentine, and bone arranged exactly as are dentine, enamel, and cementum in a mammalian tooth. The dentine, however, is chondrichthyan orthodentine with relatively few dentinal tubules of different caliber. distally dividing, and provided with lateral branchlets of minute diameter. On the crown surface there is a layer of vitrodentine with fewer dentinal tubules, and covering the entire root there is a layer of bone (fig. 52) whose morphology is the same as the bone described in the edestid shark *Ornithoprion hertwigi* (Zangerl, 1966). The bone cells, for the most part, apparently retreated as they produced the bone matrix, but a few did become enclosed within the bone substance. Their canaliculi extend in an irregular fashion from the cell bodies (fig. 52).

The shape of these teeth varies mostly as regards the length of the roots and the symmetry of the entire denticle; some are symmetrical, others strongly asymmetrical (fig. 52). The number of these denticles per specimen seems to be small.

We do not know where in or on the body these strange denticles were located. They are consistently associated with skull material and usually not intermingled with the tooth whorls. It is thus possible that they were located on pharyngeal arches.

Both roof and floor of the mouth cavity of *Sibyrhynchus* are lined with mucous membrane denticles that have basally fused to form a considerable variety of plates that have a vaguely spidery appearance. This is due to the fact that the denticles fuse along lines and the lines tend to radiate from centers (fig. 47). In the type specimen PF6408 plate and counterplate parted in such a way that one set of plates is located on the plate, while another set is located on the counterplate, the denticulated surfaces facing one another. This provided the clue that these plates, indeed, lined the mouth cavity, not the outside of the head, and made possible the decision as to which set of plates covered the roof, which, the floor of the mouth cavity.

On the roof of the mouth there are a pair of larger plates, sharply asymmetrical, surrounded by a swarm of

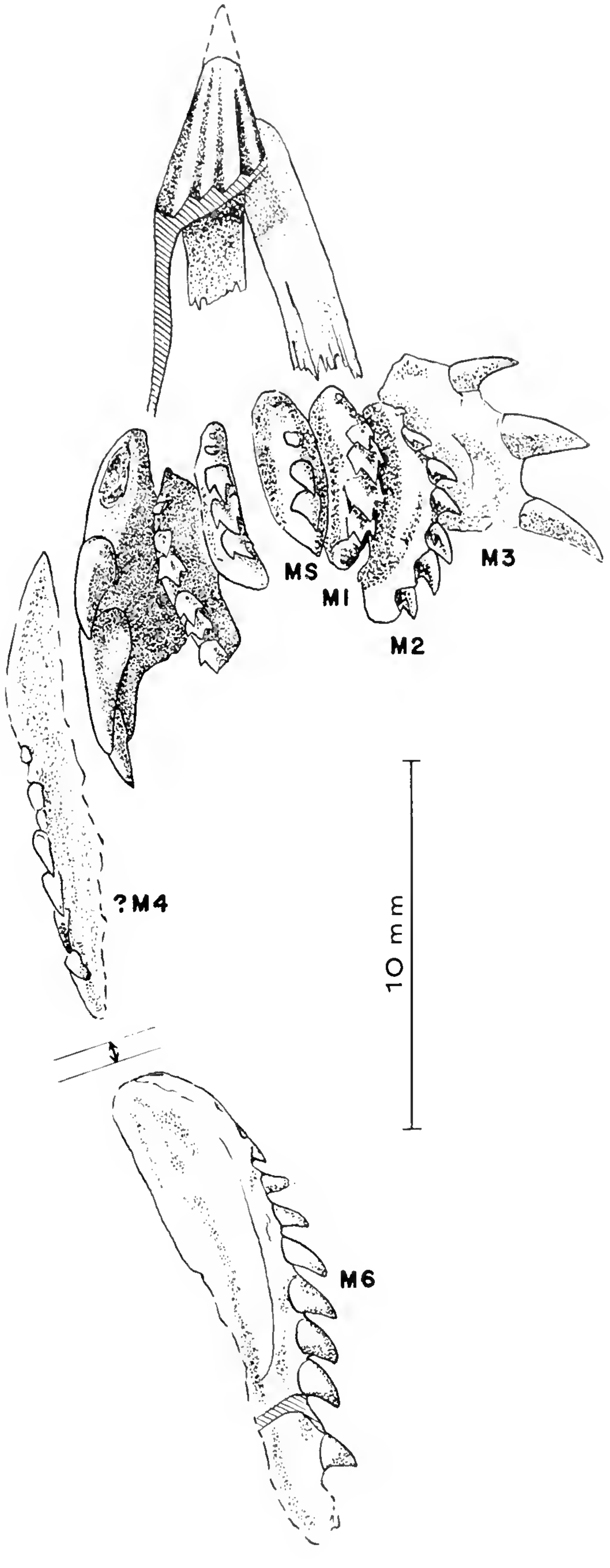

FIG. 49. Camera lucida drawing of a latex cast of the lower jaw of *Sibyrhynchus denisoni*, PF6650, which shows the anterior tooth whorls in position and perhaps also two of the lateral tooth whorls.

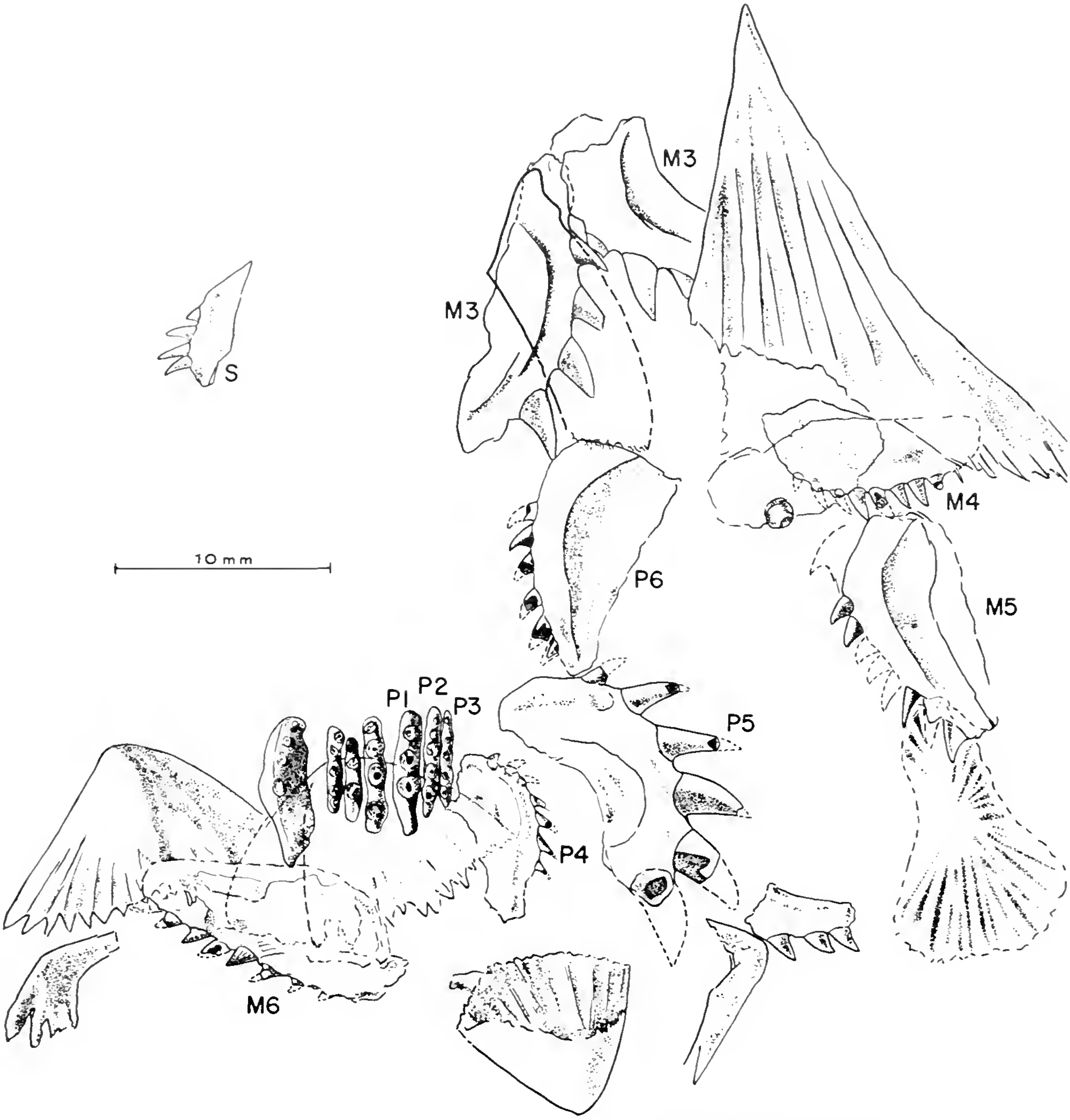

FIG. 50. Camera lucida drawing of tooth whorls and snout tubercles of *Sibyrhynchus denisoni*, PF2594. Tooth whorls of the upper jaw are in place, though the tooth crowns are all broken off.

smaller "spiders." In all probability they filled the space between the tooth whorls (fig. 45). On the floor of the mouth there is an anterior element of highly characteristic shape. It consists of an anterior, fairly thick, smooth portion followed by a fan of radiating denticle lines (fig. 47). This element is followed by at least three, fairly large, "spidery" plates. The skeletal supports of these floor plates of the mouth cavity lie between the rami of the mandible, hence are parts of the hyobranchial apparatus. A sketch showing the possible relations is shown in Figure 46.

VERTEBRAL COLUMN:

The vertebral column is partially articulated in PF6615 (fig. 53), at least in the region of the caudal peduncle. The neural arch pieces appear to be much as in *Iniopteryx*, but the ventral arcuals differ considerably from those of the compared genus in that there are curious ?fused pieces in the region back of the pelvic girdle (fig. 53) and in the tail peduncle the ventral arcuals have the shape of haemapophyses. We do not know whether the seemingly fused arcuals mentioned above represent an abnormal, or even pathological condition, or whether they are a part of the normal morphological differentiation of the vertebral column in this animal.

None of the specimens shows evidence of an unpaired dorsal fin. The tail fin is partly preserved in PF6506. Its structure is very similar to that in *Iniopteryx*, but it appears to be relatively sturdier and larger in *Sibyrhynchus* (fig. 54).

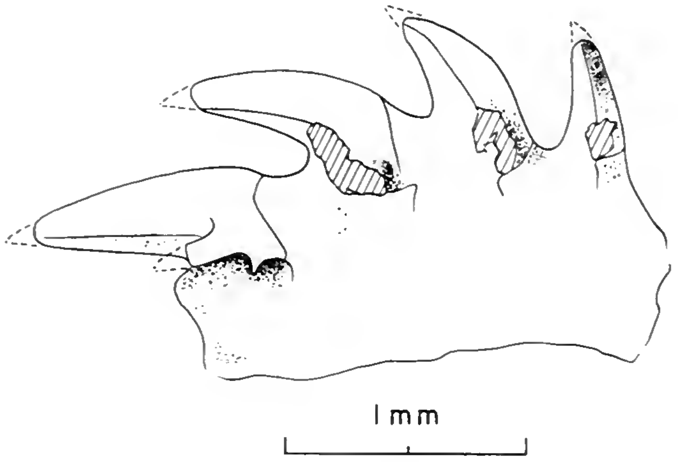

FIG. 51. Camera lucida drawing of small, probably anterior tooth whorl of *Sibyrhynchus denisoni*, PF6617, showing lateral cusplets.

SHOULDER GIRDLE AND PECTORAL FINS:

Several specimens show parts of the pectoral fins, but in all of them the finrays are broken into small pieces so that only the principle can be determined. The shoulder girdle cartilage is strongly curved and extends ventrally forward beneath the skull. It is much more massive in its dorsal half where the basal fin cartilage articulates (figs. 53, 55). The latter is well preserved in PF2632 (fig. 55). This cartilage is an approximately rectangular piece provided near one end with a strong articular head and opposite this is a deep articular pit. The fin has at least three rays of nearly equal diameter. The first, even in males, is not much larger than the others, but it does bear hooks on little bases as in *Promexyele peyeri*; the number of hooks is much smaller than in this genus. There are approximately 40 hooks on each side in addition to perhaps an equal number of very tiny hooks on the distal parts of the fin ray that cannot be counted adequately.

PELVIC AREA:

The pelvic area is well represented in a number of male individuals (PF6408, PF6506, PF6615, and PF6639). The pelvics are vaguely boomerang-shaped cartilages to which the basipterygia of the pelvic fins are attached. The latter are triangular, but in no case sharply outlined and hence perhaps were poorly calcified in life. The clasper mechanisms, on the other hand, are well preserved. Each clasper consists of a proximal piece of cartilage of moderate length followed by a series of six pieces (the first being half as long as the proximal one) and a distal elongated rod that appears to terminate bluntly in all specimens. No terminal clasper hooks were noted in this species (fig. 56). There are five or six much enlarged tenacular hooks located on each side of the basipterygium.

Appearance in life.—The reconstruction (fig. 56) provides only an approximate notion of the appearance of this fish. Since the drawing is a composite of several individuals we are not sure that the proportions of the various parts to the whole are entirely correct. An interesting matter concerns the slanted position of the mouth cleft (fig. 56). If one articulates (on paper) the lower jaw of PF2632 with the neurocranium, the lower jaw protrudes a considerable distance beyond the front end of the snout (fig. 57). This relationship is also seen in at least 10 cases where neurocrania are associated with the lower jaws in *Iniopera* (see below). Such a relationship would oppose the front tooth whorls of the upper jaw to the denticulated plates on the copulae of the hyobranchial apparatus, which is hardly credible. All the braincases are in dorso-ventral position, and in all cases the lower jaws are disarticulated and lie nearby. Since the lower jaws became disarticulated very soon after death and settled parallel to the burial ground, they did not suffer any length distortion. The neurocrania, on the other hand, are complex, three-dimensional structures. During bacterial degradation in absolutely quiet burial microenvironments these structures collapsed in such a way that all parts were projected vertically onto the burial plane; hence all

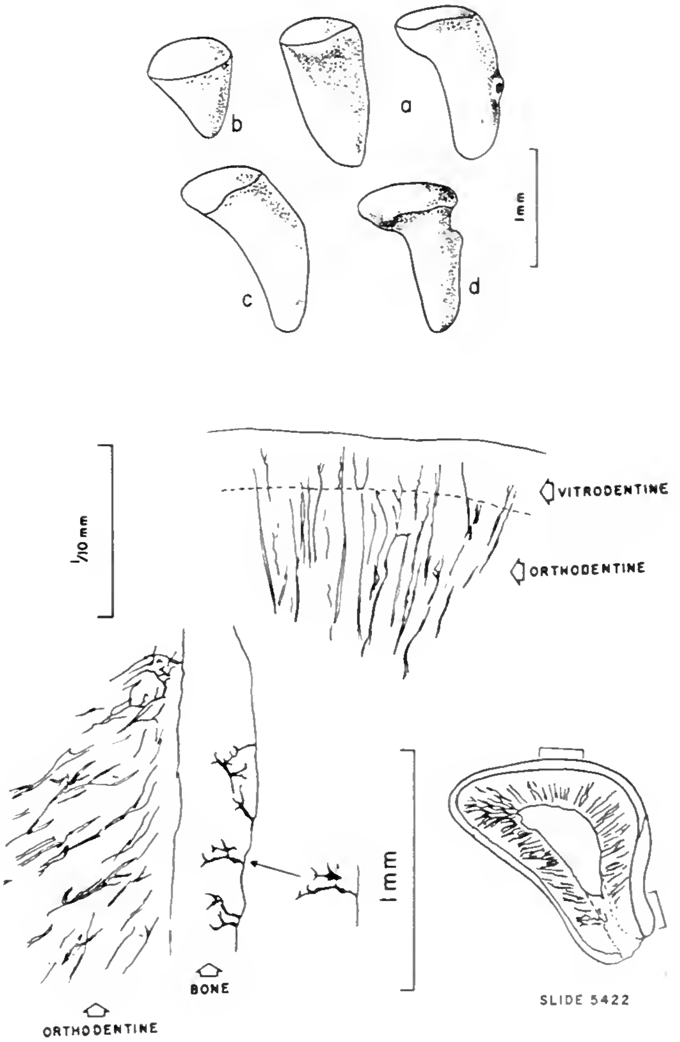

FIG. 52. ?Pharyngeal teeth of *Sibyrhynchus denisoni*, PF6617, that show very flat crowns and long roots. Thin-section, PF2918 (slide no. 5422), shows a longitudinal section through one of these teeth and histological details of the vitrodentine covering the crown and the bone covering the root.

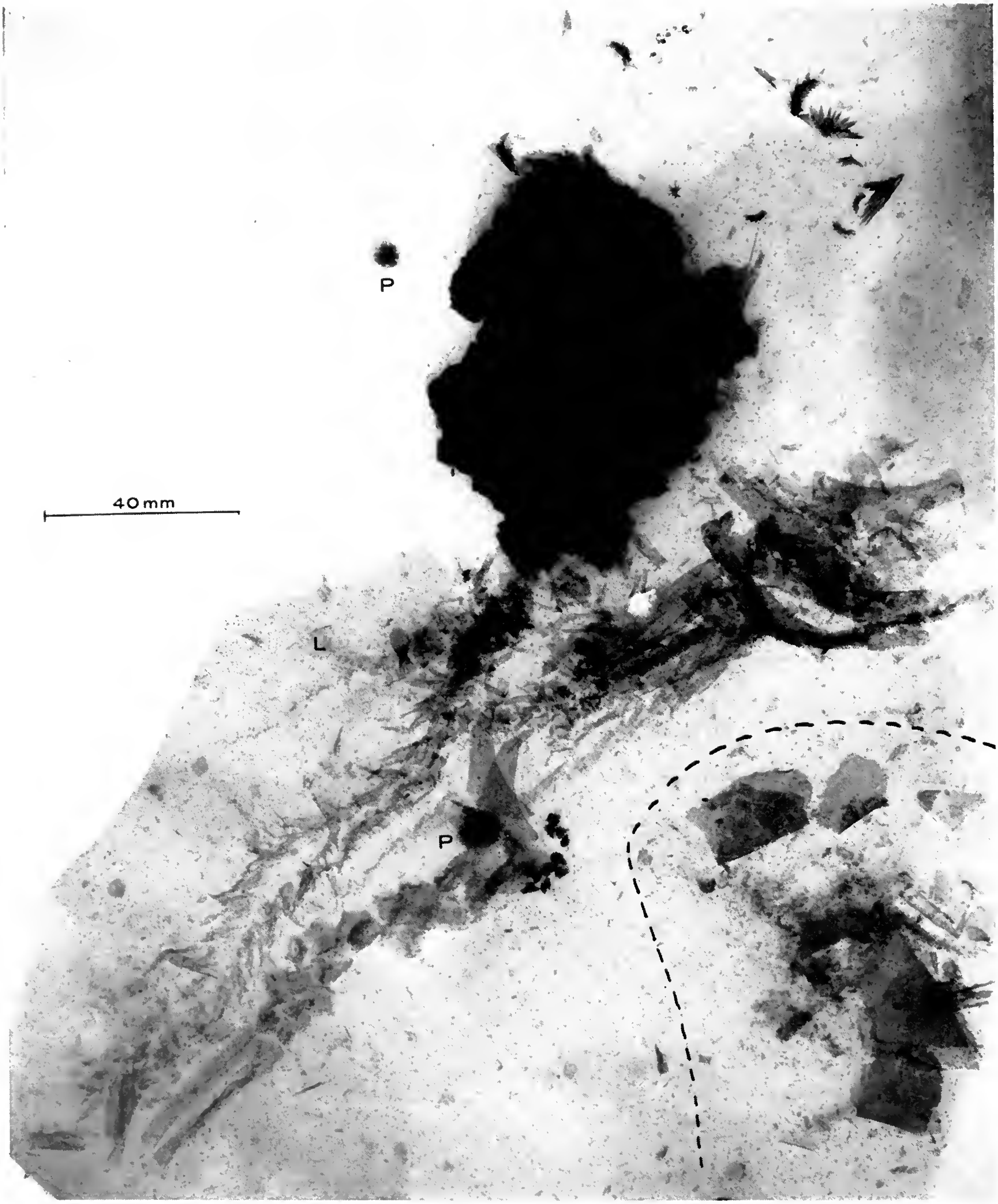

FIG. 53. Radiograph of *Sibyrhynchus denisoni*, PF6615. The neurocranium is enveloped in a thick mass of pyrite. In upper right corner characteristic snout tubercles of this species and some tooth whorls are shown. Below pyrite mass, elements of the hyobranchial apparatus, the pectoral fins, the pelvic cartilages with two clusters of large tenacular hooks, the clasper mechanism, and a partially articulated vertebral column showing peculiar fusions (?) in the pelvic area can be seen. P=*Petrodus* denticles and L=*Listracanthus* denticle, not associated; area enclosed by dashed line contains a chewed tail fin of the shark *Agassizodus*, probably on a different bedding plane.

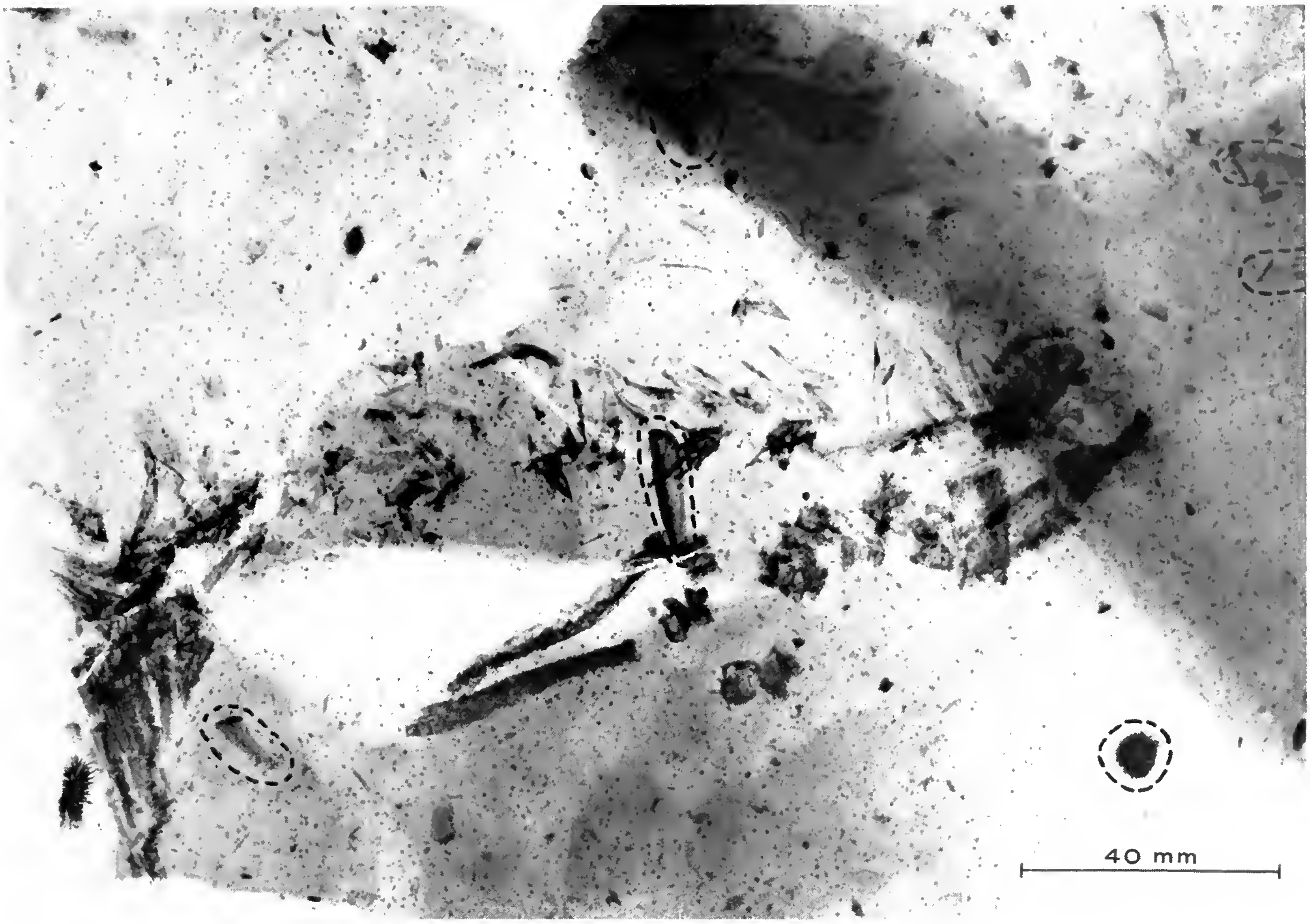

FIG. 54. Radiograph showing the posterior half of a skeleton of *Sibyrhynchus denisoni*, PF6506, with part of the tail fin. The clasper mechanism is characteristic for this species and permits its identification. Elements circled in dashed lines do not belong to this specimen.

dimensions, save those of structures parallel to the burial plane, are diminished. Upper and lower jaws in *Sibyrhynchus* and *Iniopera* could have matched in length only if one assumes that the mouth was slanted at an angle to the horizontal (fig. 58). We have tried both an upward and downward slant and have concluded that an upward slant is the more probable.

Food.—There is no direct evidence of food associated with any of the specimens, but the nature of the dentition would suggest this to have been a notable predator. The tubercles at the tip of the snout and lower jaw no doubt protected these important parts very well, but it is difficult to appreciate against what hazard.

Geographical and ecological considerations.—*Sibyrhynchus denisoni* is a common species in all the eastern localities of the Illinois basin, and very few have so far been collected in Iowa or Nebraska. It can be expected, however, to occur there as a rare stray, just as *Iniopteryx rushlaui* occurs very rarely in Indiana. A large number of *Sibyrhynchus* specimens occur as gastric residues of sharks, which indicates that in spite of its tubercles and its sharp teeth it served as prey at least as readily as other species of iniopterygians.

Genus **Iniopera**[1], gen. nov.

Characterization.—Durophagous iniopterygians with a double symphyseal whorl (fusion of two adjacent elements) in the lower jaw and a single symphyseal in the upper; in the lower jaw the third whorl from the symphyseal is differentiated as a "canine" whorl; in the upper jaw there are two "canine" whorls in positions 3 and 4 from the symphyseal whorl. Teeth extensively fused not merely at base, but for much of the crowns as well. Teeth blunt except in juveniles; whorls often smooth on functional side; lateral whorls denticulate posteriorly along ridge, smooth anteriorly, and medial sides of whorls denticulate in an oblique labio-lingual row pattern. Snout armored with a small median and two large lateral tubercles; lower jaw bears in front two large, conical tubercles. The floor of the mouth cavity armored with an anterior plate shaped like a three-sided pyramid, and a posterior element shaped like a pelecypod shell. The roof of the mouth cavity is paved with at least two pairs of plates; the larger, posterior ones being rectangular in outline, with pointed processes antero-medially. All of these plates are tuberculated

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[1] From *inion*=nape, and *pera*=leathery pouch.

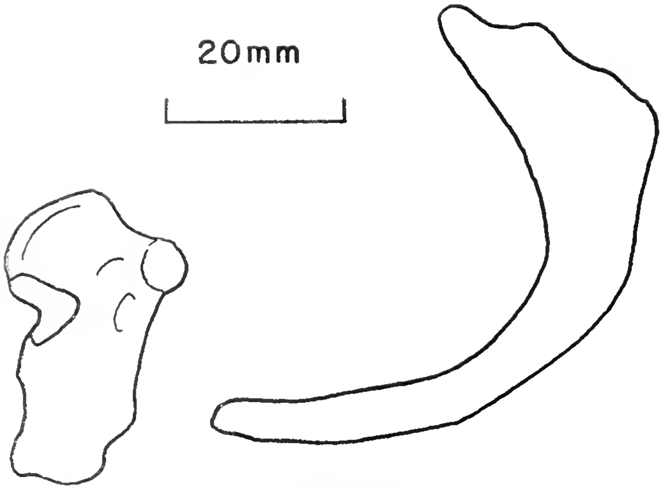

FIG. 55. Scapulocoracoid and basipterygium of the pectoral fin of *Sibyrhynchus denisoni*, PF2632.

the tubercles being mucous membrane denticles fused at the base, which becomes fairly thick in large specimens.

Pectoral fins of presumably adult specimens with large, distally pointed sacs, containing a lithified fluid similar in appearance to the fossil ink in Liassic dibranchiates from Holzmaden.

Pelvic fins probably relatively small, but clasper mechanism consisting on either side of four short anterior sections followed by an elongated piece and a sharply pointed, terminal section consisting of bone (or perhaps dentine) and containing a central canal. No terminal clasper hooks.

Type species.—*Iniopera richardsoni*, n. sp.

Iniopera richardsoni[1], sp. nov.

Type.—FMNH PF2356, ♂, skull and pectoral region in partial side position. XR:LQ229.

Horizon and locality.—Logan Quarry shale, Lower Wiley cyclothem (Staunton formation), Westphalian C, Pennsylvanian.

Logan Quarry, level G. NE-¼, SW-¼, Sec. 9, T16N, R8W, Reserve Township, Parke County, Indiana, about 1¾ miles east of West Union (Zangerl and Richardson, 1963, fig. 15).

Referred specimens.—

WEA SHALE

RICHFIELD

PF6654, ♂, articulated, partial skeleton, (W. D. White)
PF6655, ♂, partial skeleton, (W. D. White)
PF6685, —, small, partial skull, (G. R. Case)
PF6690, —, gastric residue, (G. R. Case)
PF6749, —, gastric residue, (G. R. Case)

PAPILLION

PF6656, ♂, articulated, partial skeleton, (W. D. White)
PF6699, —, tiny head and shoulder region, (G. R. Case)
PF7205, ♂, articulated juvenile specimen, (W. D. White)
PF7204, ♂, articulated, partial skeleton, (W. D. White)
PF7209, ♂, articulated partial juvenile skeleton, (W. D. White)
PF7210, ?♂, partial skeleton, (W. D. White)
PF7212, ♂, good, partial skeleton, (W. D. White)
PF7124, ♂, good, partial skeleton, (W. D. White)
PF7185, —, juvenile specimen, incomplete, (W. D. White)

STARK SHALE

FT. CALHOUN

PF6692, —, part of skull, (G. R. Case)
PF6695, —, skull and lower jaw with tooth whorls in place; juvenile individual, (G. R. Case)
PF6697, —, part of skull, (G. R. Case)

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[1] Named for the late Maurice L. Richardson, MD, of Lansing, Michigan who generously supported paleontological research at Field Museum for many years and who had an active interest in the fossils from the black shales of Indiana.

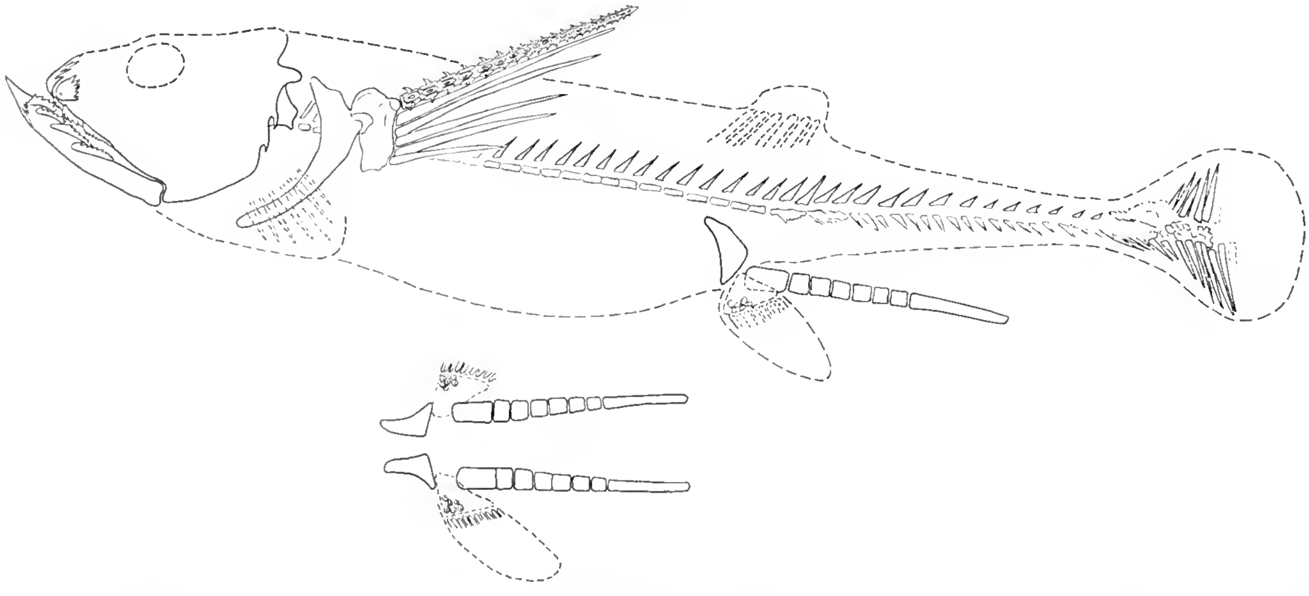

FIG. 56. Tentative reconstruction of the skeleton of *Sibyrhynchus denisoni* in side view. The proportions of the different parts of the skeleton are only approximately correct. Below, pelvic complex of male in ventral view.

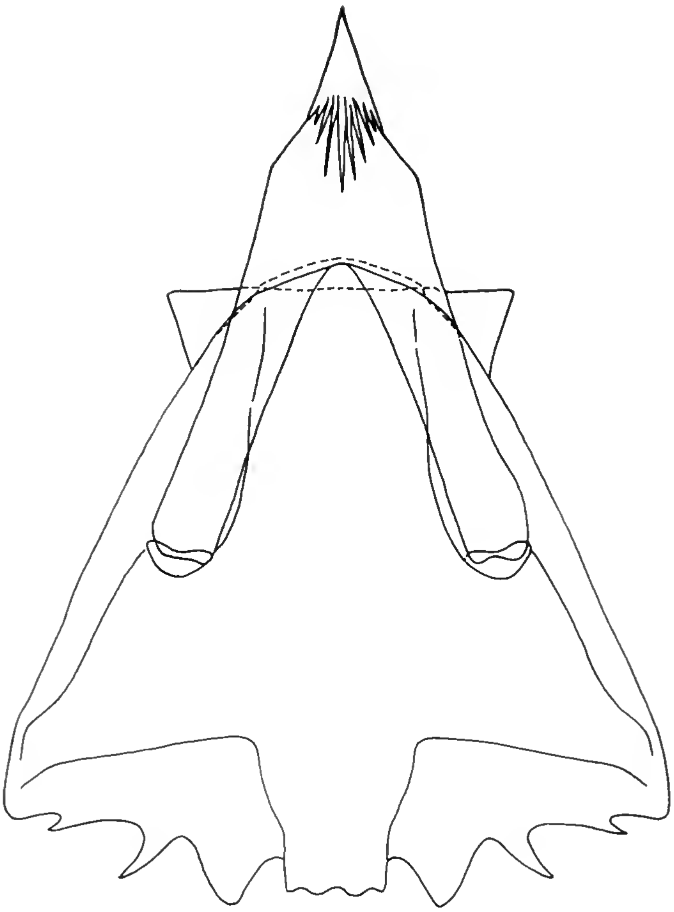

FIG. 57. Discrepancy in the length of the mandible and the neurocranium forward of the jaw articulation. The specimen depicted is PF2632, but similar discrepancies have been observed in several specimens of *Sibyrhynchus* and *Iniopera*. For an explanation see text and Figure 58.

Excello shale

Bethel Church

PF6426, ♂, partial skeleton, partly articulated, XR: Bethel 3

PF6443, ♂, very juvenile specimen, mostly disarticulated, XR: Bethel 7

PF6498, ?♂, good, partial skeleton, small individual; XR: Bethel 15

PF6499, —, gastric residue, XR: Bethel 9

PF6505, —, disarticulated skeleton, partly very good, XR: Bethel 24

PF6507, —, partial skull, lower jaw, XR: Bethel 25

PF6512, —, partial skull disarticulated

PF6526, ♂, chewed individual, XR: Bethel 57

PF6527, ♂, partial skeleton, has both pectoral pouches, XR: Bethel 17

PF6528, ♂, gastric residue (juvenile), XR: Bethel 19

PF6530, —, gastric residue, containing possibly two specimens of different size, XR: Bethel 18

PF6533, ♂, good partial skeleton, XR: Bethel 35

PF6534, —, nearly entire, articulated skeleton of juvenile, XR: Bethel 37

PF6535, ?♀, fair skeleton, weathered

PF6553, ♂, nearly complete skeleton including skull in side position, XR: Bethel 46

PF6554, ♂, good anterior half of skeleton, XR: Bethel 48

PF6591, ♂, minced specimen, XR: Bethel 41

Barret Cemetery

PF6449, —, chewed skull and shoulder, XR: Barret 4

PF6454, ♂, partial skeleton, XR: Barret 10

PF6465, —, gastric residue, XR: Barret 13

PF6550, ♂, gastric residue

PF6561, —, anterior part of skeleton, disturbed, XR: Barret 16

PF6564, —, two specimens (both chewed) on different bedding planes; specimen with braincase carries number, XR: Barret 19

PF6612, —, tiny, chewed specimen with good lower jaw, XR: Barret 27

Pit 14

PF6540, ♂, chewed partial skeleton, XR: Pit 14, No. 11

PF6542, —, disarticulated skull, XR: Pit 14, No. 5

PF6569, —, minced specimen

Mecca Quarry Shale

Mecca Quarry

PF2807, ♂, skull and shoulder, rasp hooks in place; Mecca quarry, level B4.1, XR: MQ 34

PF2825, —, partial skull; Mecca quarry level A3.1, XR: MQ 191

PF2898, —, skull disarticulated, good lower jaws; juvenile, Mecca quarry, level A4.3, XR: MQ 204

PF2899, —, disarticulated skull, Mecca quarry level B1.1, XR: MQ 72, 73

PF2902, —, gastric residue, Mecca quarry, level A4.4

PF2905, —, gastric residue, Mecca quarry, level A4.1 XR: MQ 53

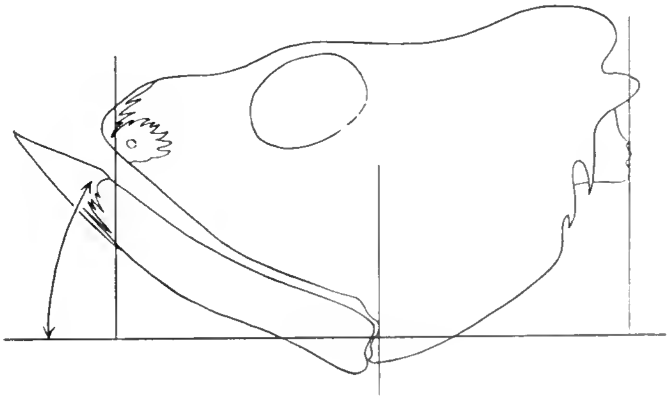

FIG. 58. Explanation of the discrepancy of the length of the mandible and the forward portion of the neurocranium which is indicated on the horizontal line. For a full explanation see text.

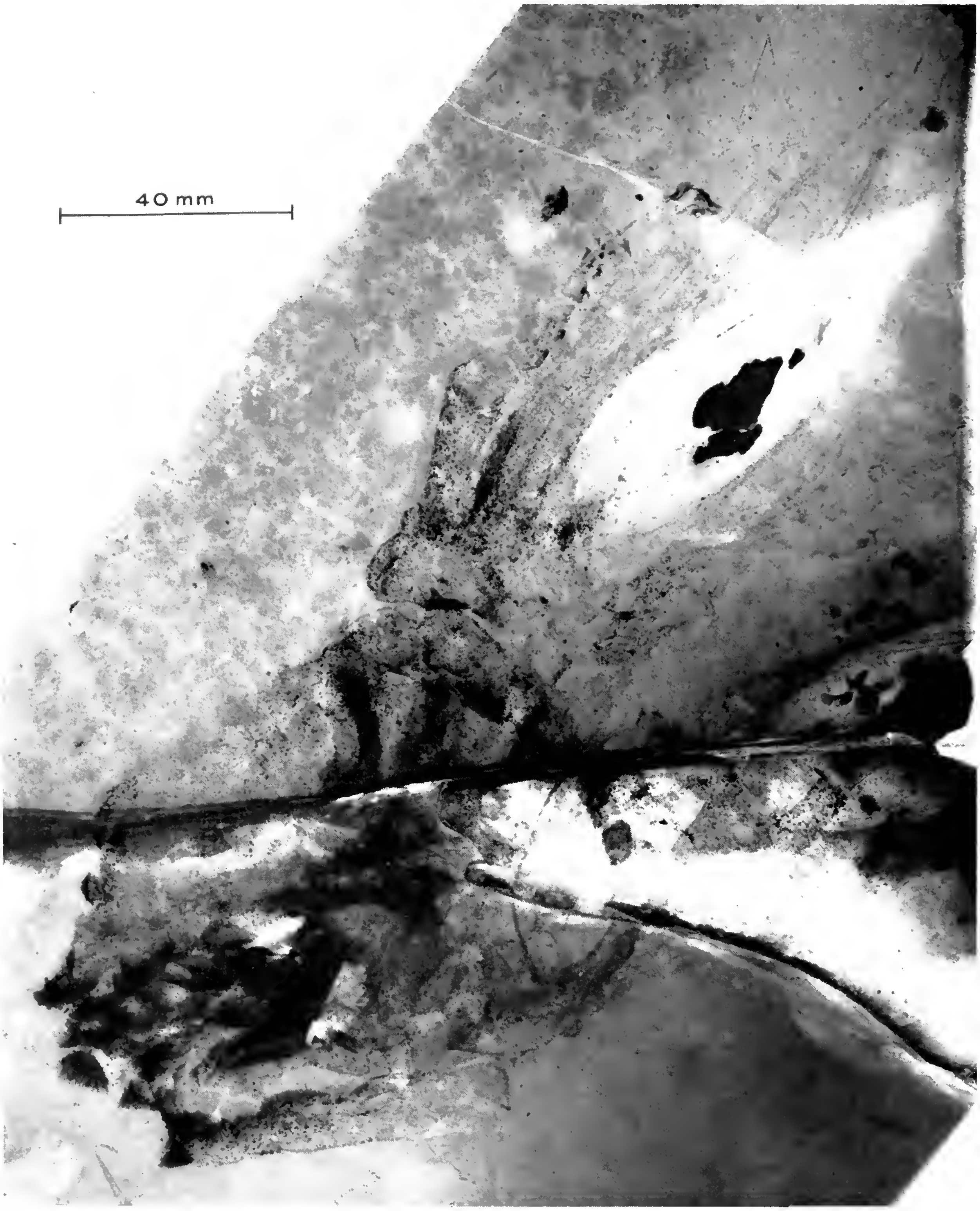

FIG. 59. *Iniopera richardsoni*, PF2356 (holotype). Positive radiograph of specimen approximately in side position (see also fig. 64).

PF2919, —, gastric residue, pectoral fin pouch, Mecca quarry level B2.4

PF2924, ♂, gastric residue containing numerous elements of this species as well as arm hooks of a ? cephalopod; Mecca quarry, level A3.2, XR: MQ 194

PF2925, —, gastric residue; Mecca quarry, level A2.2, XR: MQ 173

PF2931, —, good disarticulated specimen, braincase, lower jaw; Mecca quarry, level B2.2, XR: MQ 77

PF2932, —, excellent, disarticulated skull, partial; Mecca quarry, level B2.1; XR: MQ 22

PF2934, —, gastric residue; Mecca quarry, level B1.4; XR: MQ 164

PF2937, —, gastric residue; Mecca quarry, level B1.2

PF6659, ♂, isolated rasp hooks with large star-shaped bases; Mecca quarry, level A2.4

PF6717, ♂, gastric residue; Mecca quarry, level B1.1

PF6726, —, gastric residue containing *Iniopera* and paleoniscoid remains; Mecca quarry, level B1.1; XR: MQ 211

PF6737, —, gastric residue; Mecca quarry, level A1.3

PF7115, —, gastric residue containing pectoral fin pouch; Mecca quarry, level B2.4

CL154, ♂, anterior half of skeleton, articulated. XR, Property of Mr. John Carlson. Recovered from lateral extension of Field Museum's Mecca Quarry

U.S. HIGHWAY 41

PF1021, —, partial skull. XR: Disc. Site 16

MONTGOMERY CREEK

PF6626, —, good, small lower jaw with tooth whorls in place.

PF6624, —, scattered elements. XR: Montgomery Creek 4

SPENCER CREEK

PF6625, —, disarticulated skull. XR: Spencer Creek 2

WEST MONTEZUMA

PF6622, ♂, anterior two-thirds of an articulated skeleton with pouch fills. XR: Montezuma 1–3

PF6630, —, disarticulated specimen

PF6631, —, disarticulated specimen

PF6638, —, disarticulated specimen

PF6640,—, anterior two-thirds of articulated specimen with pouch fill

ARKETEX

PF6739, —, part of a cranium. XR: Arketex-2

OTTER CREEK

PF6589, —, disarticulated skeleton with both pouch fills. XR: Otter Creek 5

CHINOOK MINE

PF5886, ♂, disarticulated skeleton. XR: Chinook 8

PF5889, —, disarticulated skeleton, XR: Chinook 10

LOGAN QUARRY SHALE

LOGAN QUARRY

PF2353, —, part of a mandible and ?neurocranium. Logan quarry, level G. XR: LQ 275

PF2359, ♂, large part of excellent skeleton, Logan quarry, level J. XR: LQ 92

PF2593, ♂, disarticulated skeleton, Logan quarry, level G.

Characterization.—Same as for genus.

Description.—*Iniopera richardsoni* is a common, highly characteristic element of the Mecca fauna. Its skeleton is the most highly sclerotized of all iniopterygians, the dentition being durophagous and thus relatively massive, and the mouth plates and snout tubercles relatively thick; the end sections of the claspers are sclerotized and there is evidence of dermal armor in the form of pavements of denticles in the head region and scattered ones in the form of little "snowflake" denticles over part of the body.

FIG. 60. Much enlarged (negative) radiograph of the peculiar, radio-opaque substance within the pouch fills of *Iniopera richardsoni*, PF2356 (see fig. 59).

A most peculiar feature of this form is the presence of a pair of mostly membranous pouches (fig. 59), associated with the pectoral fins, which contain a highly organic, lithified substance that breaks with conchoidal fracture and resembles somewhat the lithified ink in the ink sacs of Jurassic dibranchiates. Not every specimen shows these pouches, and their size appears to have little to do with the size of the animal (except that small individuals never show them). It is thus probable that the size of the pouches depends on the amount of substance (probably a fluid) that they contained at the time of death, not on the age of the individual. So far, all specimens that show pouches are males. Furthermore, the pouches of the type specimen PF2356 each contain a fibrous patch of substance within the pouch-fill that is highly radio-opaque as seen on X-ray film, indicating

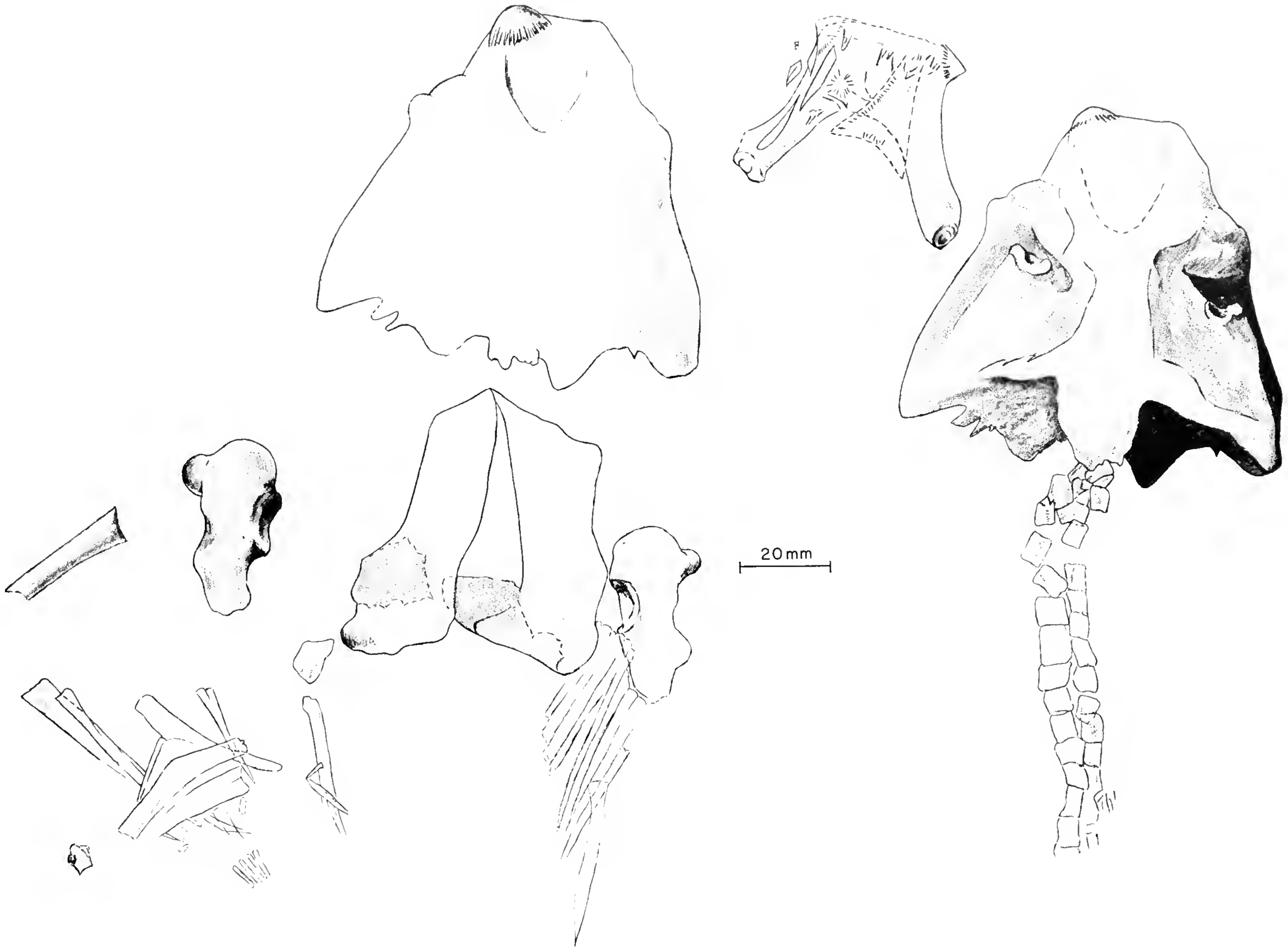

FIG. 61. *Iniopera richardsoni*, PF2359. Drawing of part of the skeleton made from enlarged stereo radiographs. The neurocranium is shown from both the dorsal and ventral sides.

FIG. 62. *Iniopera richardsoni*, PF6622. Drawing of the head region made from enlarged stereo radiographs.

that it contains an element of relatively high atomic weight (fig. 60). We have no idea what this material might represent, why it seems to be concentrated within the substance of the pouch-fill, or why it should be fibrous in structure.[1] The nature of these organs is, of course, likewise a matter of speculation at this time. They might be analogues of the ink sacs of dibranchiates; they might be poison glands or even accessory male sex glands. Less probable, though not impossible is the notion that they served as incubators for the eggs, perhaps carried by the males. The idea that they might represent parasitic infestations seems the least likely possibility.

SKULL:

Several specimens (e.g., PF2359, PF6622), show the braincase in dorso-ventral position (figs. 61, 62). In all cases one can distinguish a dorsal portion which formed the roof and sides of the brain cavity, contained the orbits and enclosed the nasal cavities, though the latter two features are never distinctly seen. In PF2359 there seems to be a broad depression in the snout region of the skull roof (fig. 61) resembling somewhat the cavum precerebrale of sharks (see, for example, Smith, 1937, pl. 1). The ventral portion of the neurocranium consists, as in other genera of this order, of a median longitudinal plate to which the vertebral column attaches posteriorly, transverse ridges that extend to the postero-lateral corners of the neurocranium and a little more dorsal (though beneath the dorsal roof), the paired sheets of calcified cartilage (? posterior parts of the palatoquadrates) that are attached to the postero-lateral corners of the neurocranium and to the medio-ventral plate, and terminate anteriorly in the articular facettes for the fused Meckel's cartilages (fig. 61). The forward portions of the palatoquadrates are so intimately united with the neurocranium that their presence can

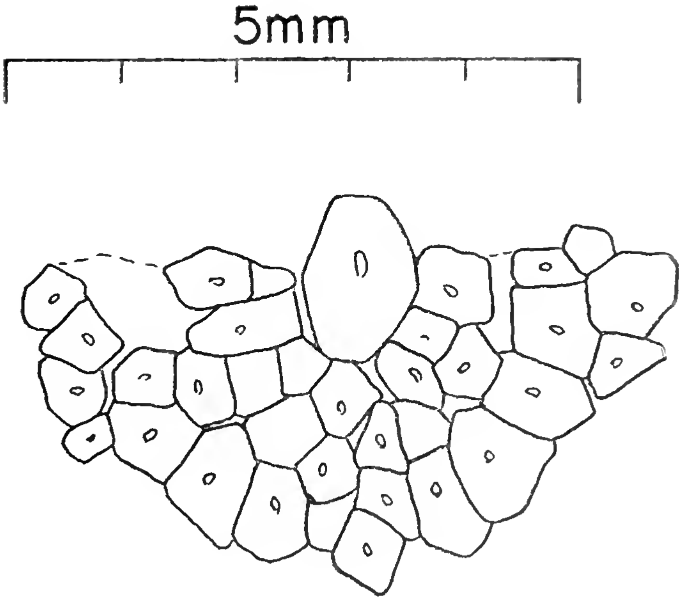

FIG. 63. Camera lucida drawing of a patch of dermal denticles that form a pavement presumably on the dorsal (or ventral) side of the head of *Iniopera richardsoni* (PF7129).

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[1] Chemical analysis is contemplated as soon as additional specimens with this feature become available.

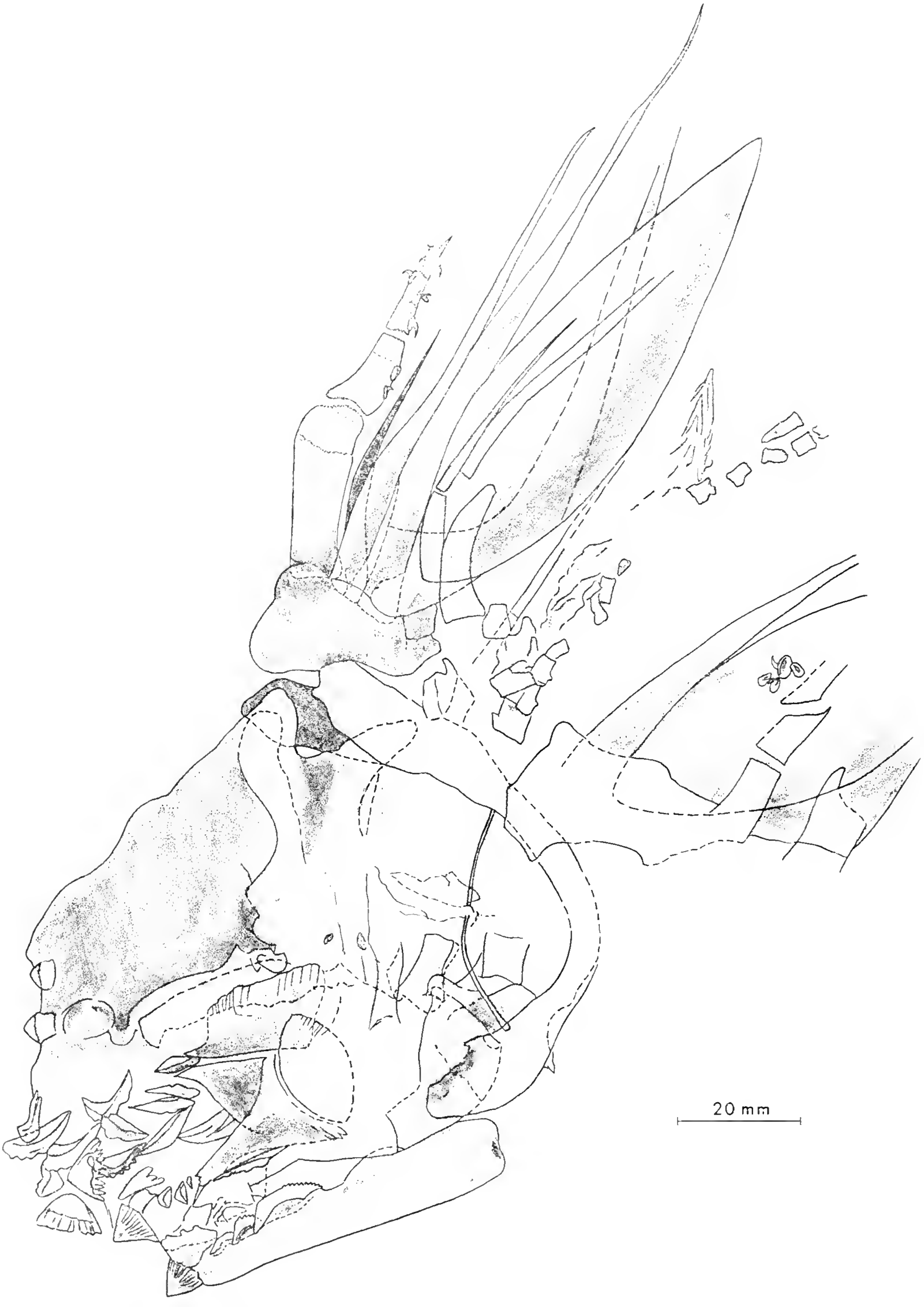

FIG. 64. *Iniopera richardsoni*, PF2356 (holotype). Drawing made from enlarged stereo radiographs (see fig. 59).

only be surmised. We assume that they form the tooth-bearing parts of the upper jaw.

The snout is armored in front by a blunt medial and two stout, lateral tubercles; additional minor tubercles may be present elsewhere on the skull and there is evidence that small dermal denticles may have dotted the skin of the head and may even have formed a pavement over the dorsal or ventral portion of the head region (fig. 63). The Meckel's cartilages are fused at the symphysis which forms a fairly broad shelf. At the antero-lateral corners there are two notably pointed tubercles (figs. 64, 65).

FIG. 65. Snout tubercles, dentition, and mouth plates of *Iniopera richardsoni*, PF2356 (holotype). Drawing made from greatly enlarged stereo radiographs. Compare with Figure 64.

The dentition is durophagous. It consists of fairly massive tooth whorls in which the individual tooth crowns are short and relatively blunt in adult individuals. Anteriorly many tooth whorls are devoid of denticles and we assume that they have been worn off (fig. 65). A longitudinal section through a tooth whorl of an adult specimen shows that the individual teeth are very extensively fused to one another, not merely at their bases, but along the sides of the crowns (fig. 66). In very small individuals the teeth composing each whorl are much larger relative to the size of the whorl and more acutely pointed than in the adult condition so that individual tooth whorls of young individuals may be mistaken for those of *Inioxyele* or even *Sibyrhynchus*.

The lateral tooth whorls are particularly interesting, because they seem to be not merely fusions of teeth belonging to single tooth families, but additionally of adjacent tooth families. This might explain why their lingual surfaces are covered with teeth in oblique, labiolingual rows (fig. 67).

The upper dentition consists of a symphyseal whorl, followed by seven pairs of whorls. The third and fourth pairs are differentiated as "canine" whorls. In the lower dentition the symphyseal element consisting of the fusion of a pair of whorls is clearly seen in a specimen in which the whorls are viewed from the underside (fig. 68). There are six pairs of whorls in the lower jaw. The third pair is differentiated as "canine." The anterior lower tooth whorls seem to be much broader and stouter than the opposing upper whorls (fig. 69).

The mouth cavity is armored with rather massive plates in the adult condition. As in *Sibyrhynchus*, these plates are the product of basal fusion of pavements of mucous membrane denticles that become dull upon wear and may disappear entirely on the most heavily worn parts of the plates (fig. 67). The shapes of these plates are characteristic for the genus. On the floor of the mouth (resting on elements of the hyobranchial skeleton) there is an anterior, triangular plate shaped like a three-sided pyramid whose posterior side is a little smaller than the two antero-lateral sides. Behind this plate there is another, shaped like a pelecypod shell with the hinge side facing forward (fig. 70). On the palate there are two rectangular plates, each bearing antero-medially a strong projection. These plates are also three-sided pyramidal, the postero-lateral side being far and away the largest. A second pair of much smaller plates is located immediately in front of the larger pair, fitting into the notches produced by the forward processes of the larger plates (fig. 71). In addition, there appear to be even smaller plates whose exact position remains to be determined (fig. 70).

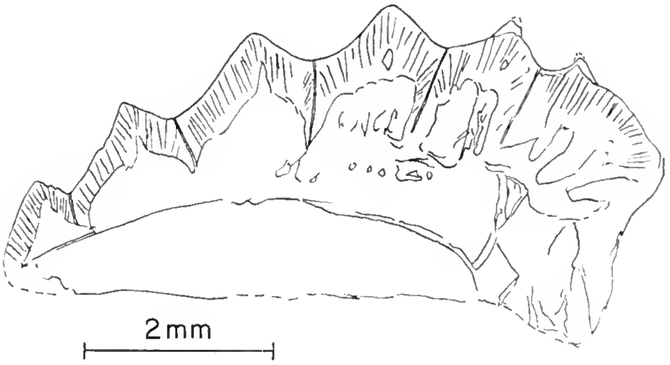

FIG. 66. Camera lucida drawing of a tooth whorl of *Iniopera richardsoni*, PF6630, that had been broken lengthwise. Note extensive fusion of denticles.

HYOBRANCHIAL APPARATUS:

The three elements, a, b, and c, of Figure 72 are very often seen isolated but associated with specimens of *Iniopera richardsoni*. Piece "a" is almost always seen in the position shown and is always asymmetrical, never paired. We thus assume that it is an unpaired, sagittal element with the sagittal plane located parallel to the paper on which it is drawn. Only very rarely are elements "b" and "c" associated with a symmetrical piece to which the three-sided pyramidal mouth plate (see above) is attached (fig. 73). As the type specimen clearly shows, the symmetrical, three-sided, pyramidal mouth plate was located in life on the floor of the mouth cavity. We, therefore, interpret the element "a" as the anteriormost element of the copula, a glossohyal. Element "b" corresponds very well with the second copula cartilage described in *Sibyrhynchus* (p.

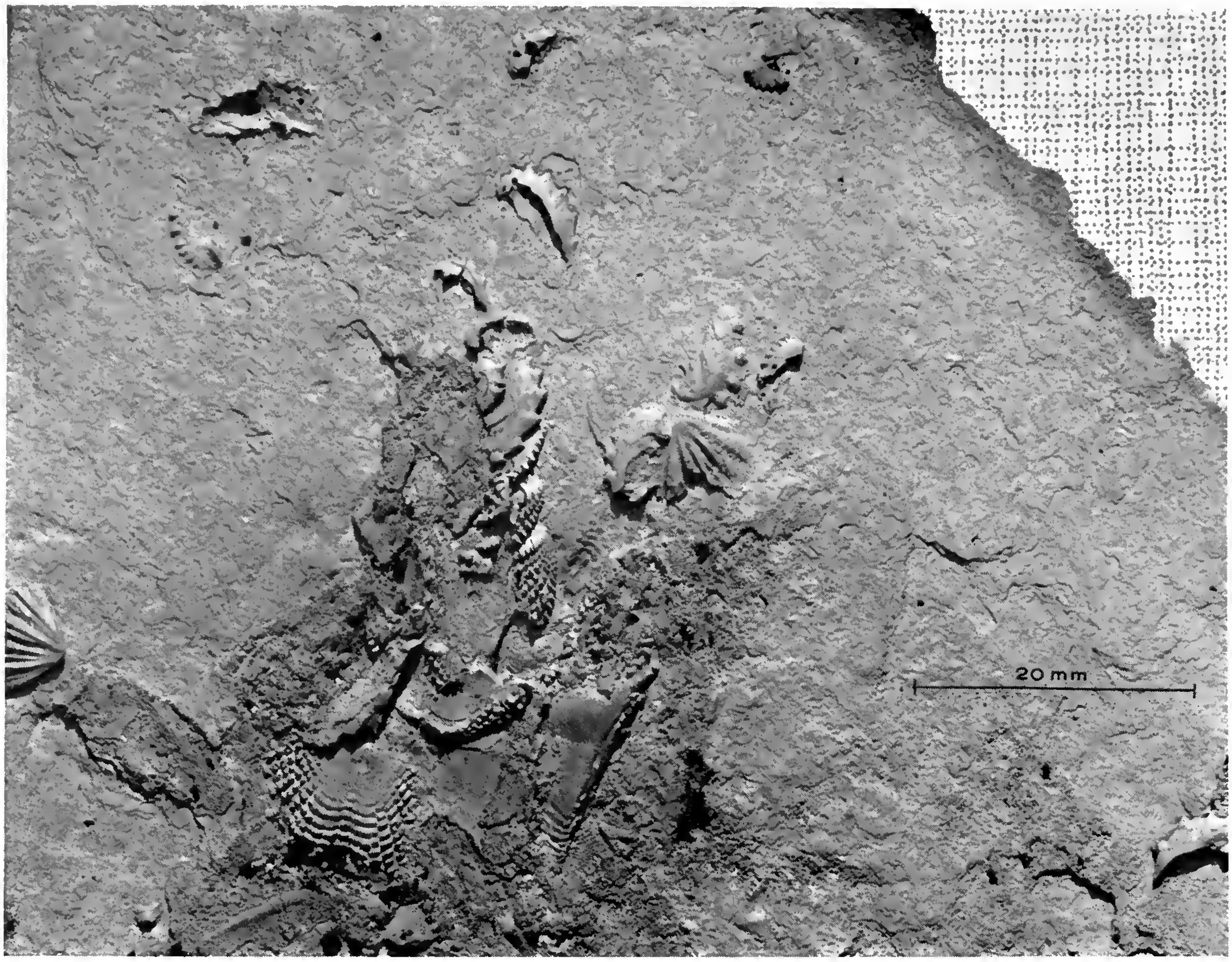

FIG. 67. *Iniopteryx richardsoni*, PF2593. Photograph of a polysulfide rubber cast (Smoothon) of part of the dentition, snout tubercles and mouth plates.

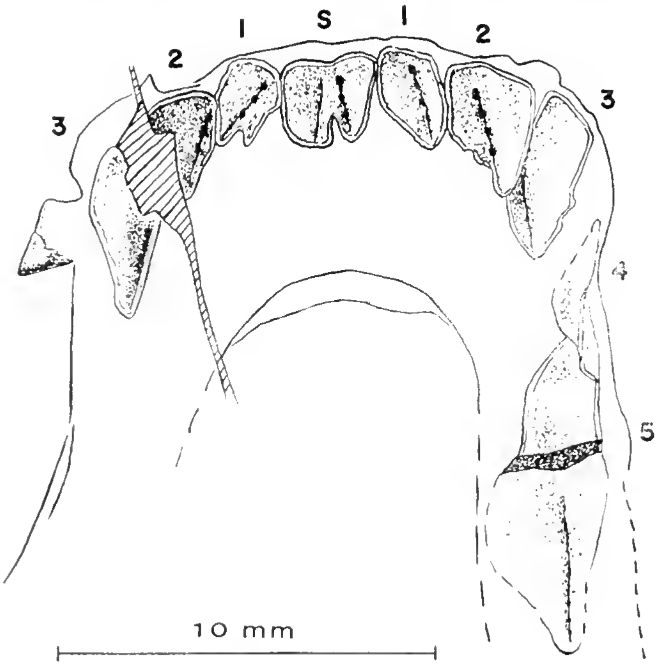

FIG. 68. Camera lucida drawing of the lower jaw of *Iniopera richardsoni*, PF 6561, in which the undersides (pulp cavity sides) of the tooth whorls are visible.

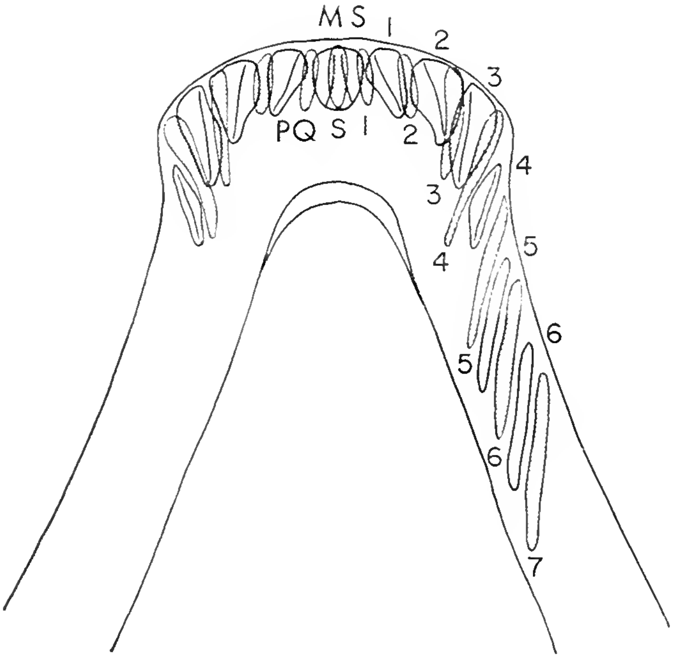

FIG. 69. Diagrammatic illustration of the dentition of *Iniopera richardsoni*.

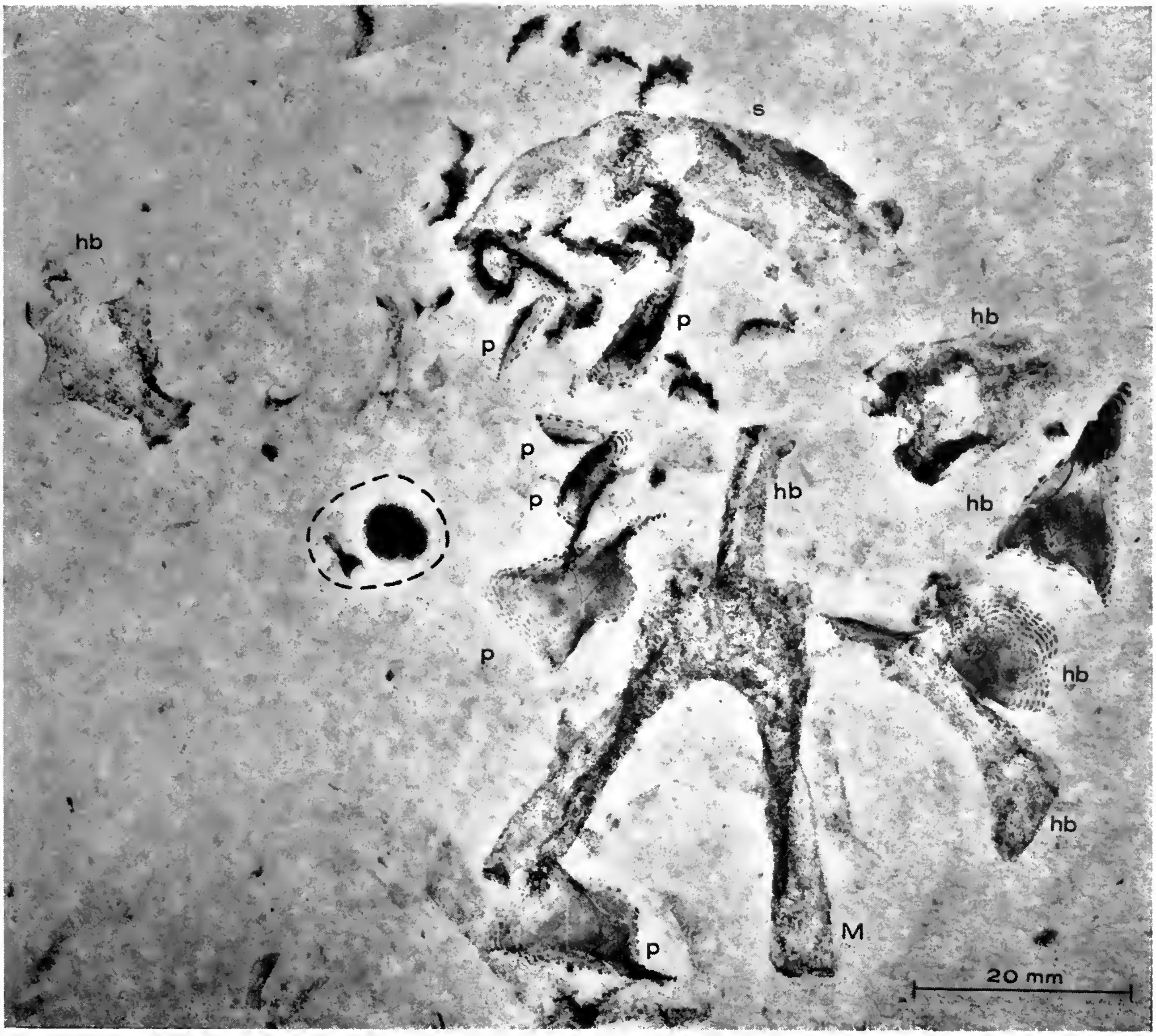

FIG. 70. Positive radiograph of a portion of the skeleton of *Iniopera richardsoni*, PF2932. **hb**, hyobranchial elements; **p**, palatal plates; **s**, scapulocoracoid; **M**, Meckels cartilages fused at symphysis. Elements enclosed in dashed line do not belong to the specimen.

38) where it is somewhat stouter than in *Iniopera*. Element "c" is also seen in *Sibyrhynchus* and is probably a ceratohyal (see p. 39).

SHOULDER GIRDLE AND PECTORAL FIN:

The shoulder girdle is a fairly massive set of cartilages with well-developed articular heads for the basipterygial articulation. In PF2359 (fig. 61) it looks as if the articular heads were at the dorsal ends of the scapulocoracoids, but this is not the case; the portions above the heads have been folded under and are thus mostly hidden (shadowed on the radiograph). The shape of the basipterygium is clearly seen in Figure 61. It is provided, at the wider end, with a pronounced articular pan for its articulation with the shoulder girdle, and a strongly protruding joint head for the articulation of the first (anterior-most) finray. The type specimen is by far the best for the description of the pectoral fins. These consist of about eight cartilaginous rays, the first of which is much enlarged and perhaps (though not certainly) segmented. It bears rasphooks of the same general construction as in *Sibyrhynchus*, *Promexyele*, and *Inioxyele*, but not in very large numbers. In contrast to other iniopterygians, the first ray is not the longest. Instead the third ray appears to be the longest (fig. 64). The fourth, fifth, and sixth rays seem to be associated with the pouch. Their curvature fits closely the curvature of the pouch, and they may have served to reinforce its membranous wall.[1]

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[1] We have interpreted the highly organic, conchoidally fracturing bodies associated with the pectoral fins of this fish (fig. 64) as lithified contents of membranous pouches because these bodies are three dimensionally preserved with sharp, smooth outlines. They are enclosed neither in calcified cartilage nor in any other kind of sclerotized tissue, but some of the fin rays were clearly applied to the outside of these bodies. Since it is not reasonable to suppose that these bodies consisted of a solid substance during the life of the animal, but rather a fluid of some sort, one is forced to postulate a membrane that would have contained the fluid (or gel) after death. Zangerl and Richardson (1963) have postulated, on different grounds, extremely rapid deposition of the black muds in which these organisms became buried. The present occurrence strongly supports that conclusion, because bacterial decomposition of a membrane in water of 21° C. (or more) is a matter of a very few days.

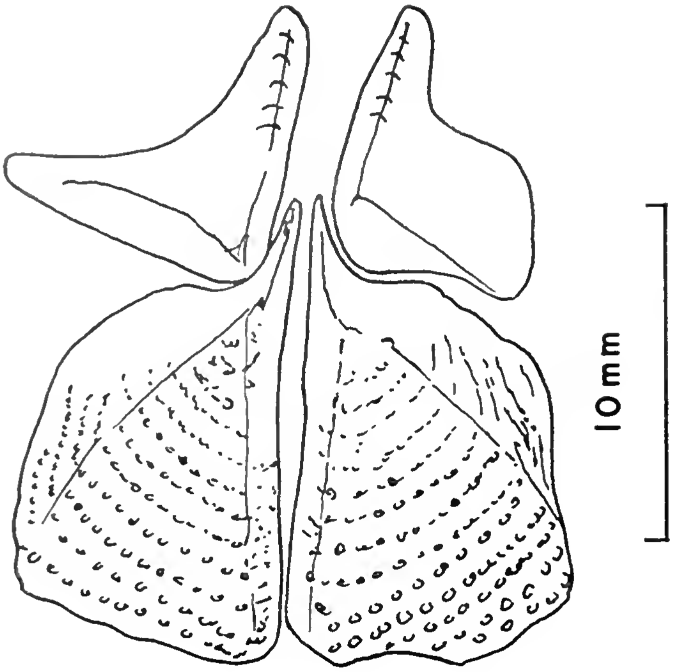

FIG. 71. Palatal plates of *Iniopera richardsoni*, PF2899, preserved in association.

In PF6622 (fig. 74), in which both pouches are present, but where the pectoral fins are not very well preserved, the pouches are much smaller than in the type specimen and behind their posterior ends there are two aggregations of fishhook-shaped denticles that look rather conspicuously like clasperhooks. When this specimen was collected, it was split through the plane of the fossil, dividing it into plate and counterplate. The split went through the pouches to expose their substance and this was enclosed, all around, by calcified cartilage. Hence we cannot be entirely sure that the pouch-fills in PF6622 are the same structures as those in the type specimen PF2356, yet these specimens surely belong to the same species. The differences noted may not be differences at all: fishhook denticles may have been present behind the pouches in the type specimen where the shale slab is so broken that the hooks may be on the missing piece of the specimen, and the split through the pouches of PF6622 may have gone across supporting finrays on both sides. The situation obviously requires clarification by additional specimens.

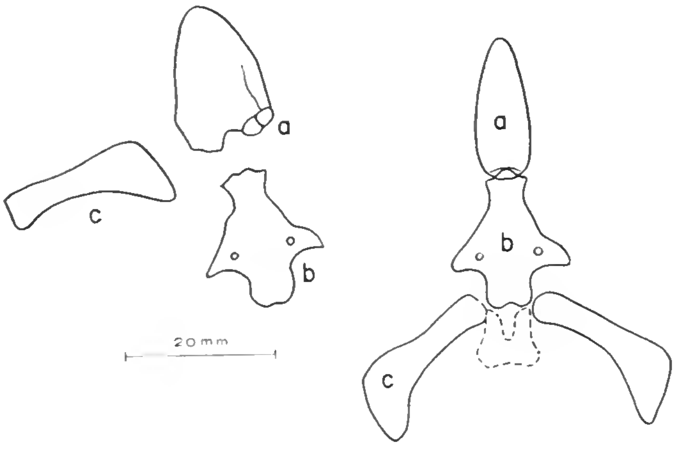

FIG. 72. Hyobranchial apparatus of *Iniopera richardsoni*.

VERTEBRAL COLUMN AND UNPAIRED FINS:

The vertebral column is organized much as in other iniopterygians. In PF2359 we see the anterior portion of the column in ventral view. This consists of two columns of ventral arcualia (fig. 61); farther back the dorsal arch pieces are more clearly seen in this specimen. In none of the presently available specimens is the entire vertebral column preserved in such a way as to permit detailed description. In PF6656 there is a partial tail fin which shows in essence the same construction as in *Iniopteryx*. Both dorsal and ventral finrays in this individual are slanted obliquely backwards, a condition that is also occasionally observed in *Iniopteryx*. We assume that *Iniopera* possessed a dorsal fin, though none of the specimens show the structure *in situ*.

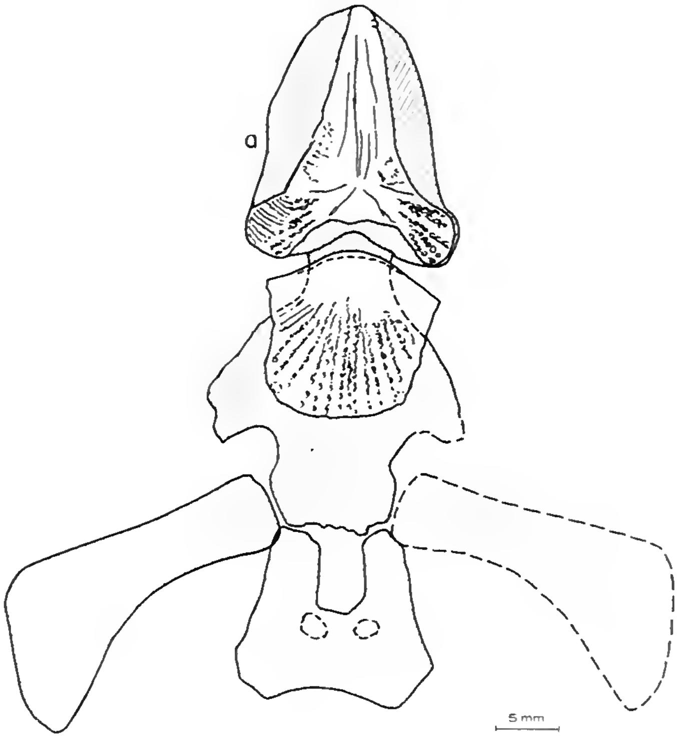

FIG. 73. Hyobranchial apparatus with superposed plates of *Iniopera richardsoni*, based on PF6638.

PELVICS AND CLASPER MECHANISM:

The pelvic cartilages are slender, relatively straight, and distally slightly enlarged elements. The basipterygia are triangular as in other iniopterygians. In the male specimen, PF6656 (fig. 75), they seem to be relatively smaller than in the presumed female, PF6535, but this may be due to less perfect preservation.

The clasper apparatus of this species is very distinctive. It is seen in PF6656 and PF7124 (figs. 75, 76). The proximal portion of each clasper consists of about four cartilaginous segments each about as long as wide (in the present flattened condition). This is

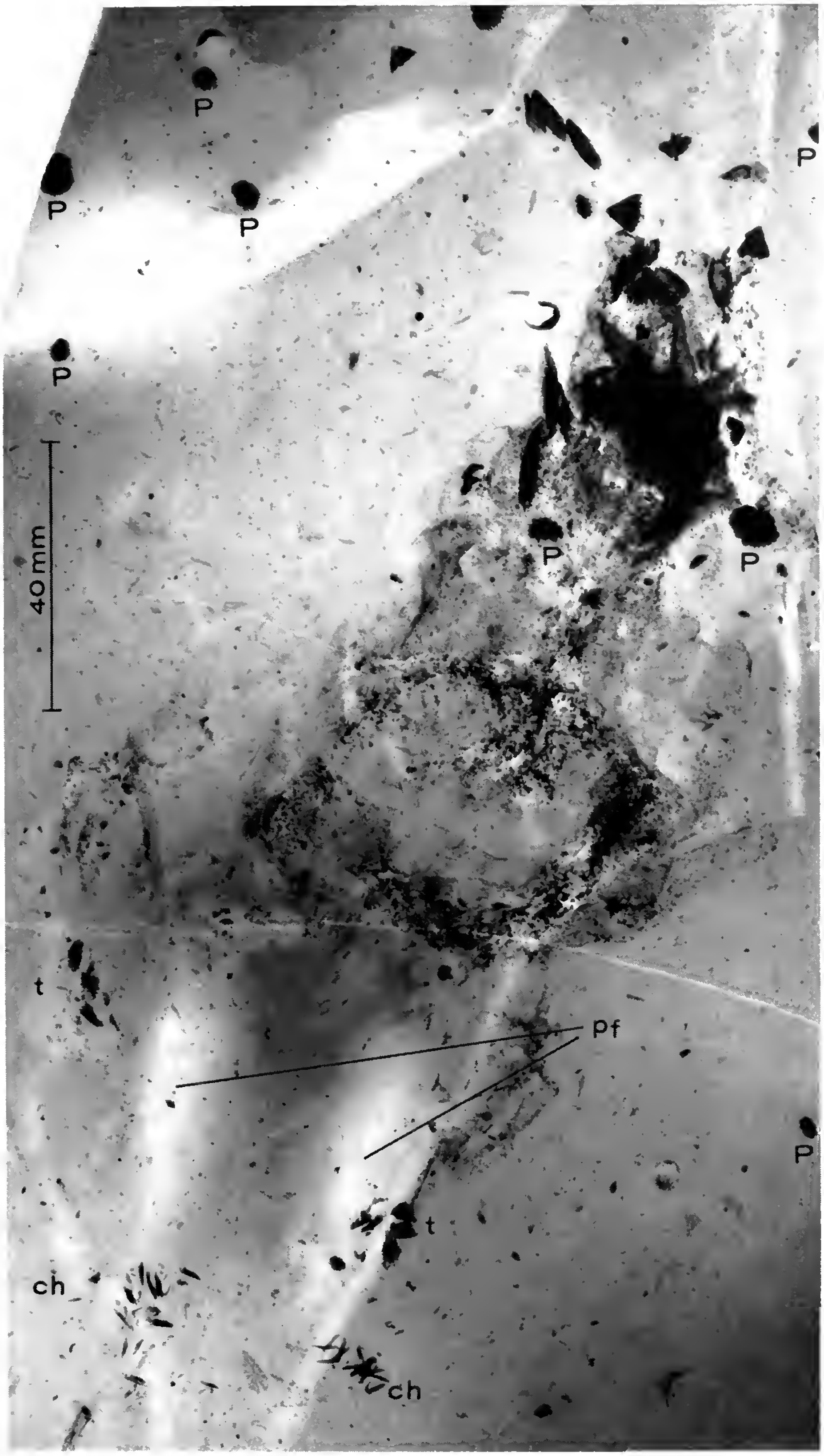

FIG. 74. Positive radiograph of *Iniopera richardsoni*, PF6622. **t**, tenacular hooks; **ch**, clasper hooks; **pf**, pouch fill. P=*Petrodus* denticles in other bedding planes.

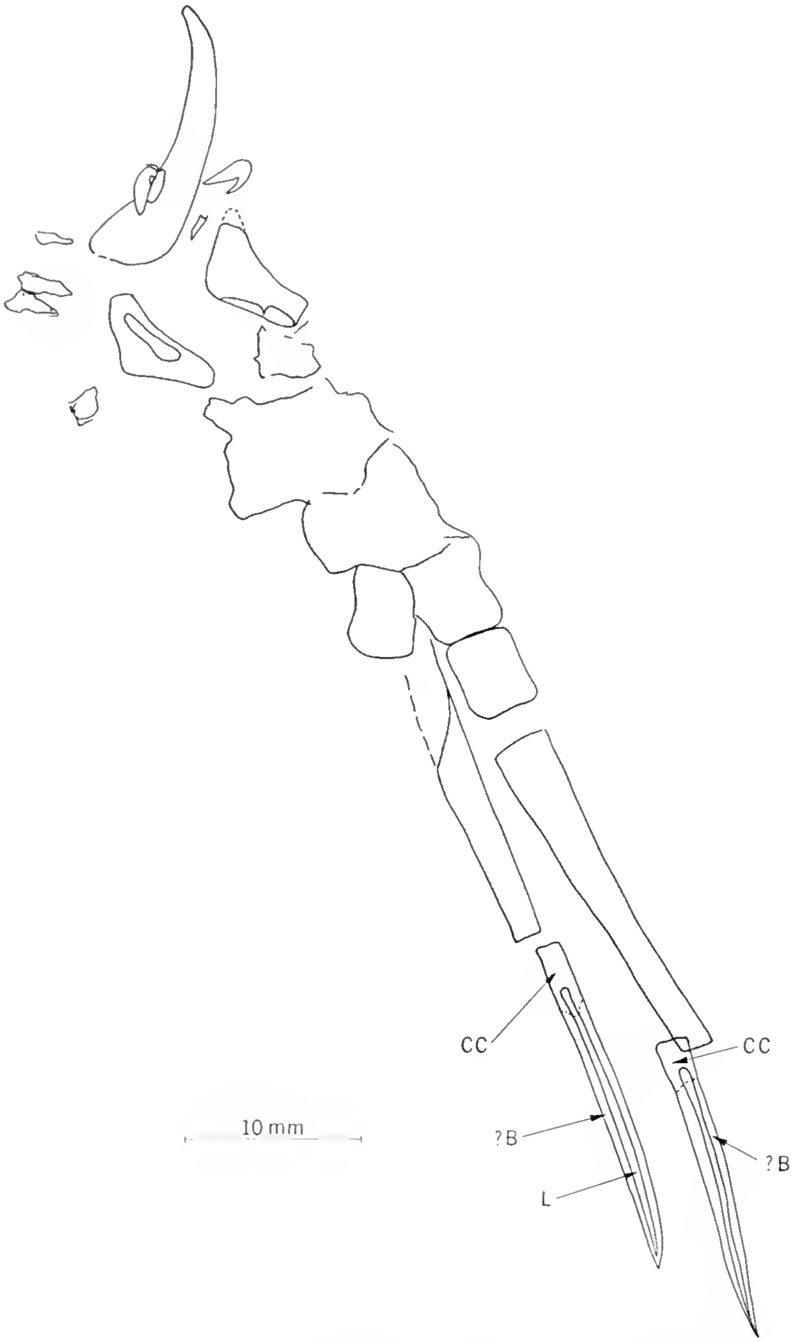

FIG. 75. Camera lucida drawing of the pelvic complex of *Iniopera richardsoni*, PF6656. Abbreviations: cc, calcified cartilage; ?B, bone or dentine; L, lumen of central canal.

followed by an elongated cartilage rod about as long as the four proximal elements taken together; the distal element is also elongated, tapering to a point. But it consists, except for its proximal end, of a material that resembles bone or dentine on the break. Because it consists of a dense, sclerotized tissue, this section of the clasper shows the central canal (fig. 75), which we assume was also present in the cartilage rods, but is not seen there because calcified cartilage collapses during bacterial decomposition. No clasper hooks were noted at the distal ends of these sclerotized clasper segments.

DERMAL DENTICLES:

It was mentioned above that there are dermal elements distributed about the head region, sometimes apparently even forming patches of pavements (fig. 63). Many specimens, furthermore, show a sprinkling of dermal denticles resembling snowflakes in the region of the abdomen; their number is not very great and it is possible that they lined the mid-dorsal or mid-ventral lines of the body. Not infrequently two such "snowflakes" are fused into a single element (fig. 77). *Iniopera* is thus the only iniopterygian in which dermal denticles occur in the skin back of the head region.

APPEARANCE IN LIFE:

Iniopera richardsoni probably presented a variety of sights to the Pennsylvanian observer, depending on whether its pouches were filled, partially filled or empty. We have attempted a reconstruction of the skeleton

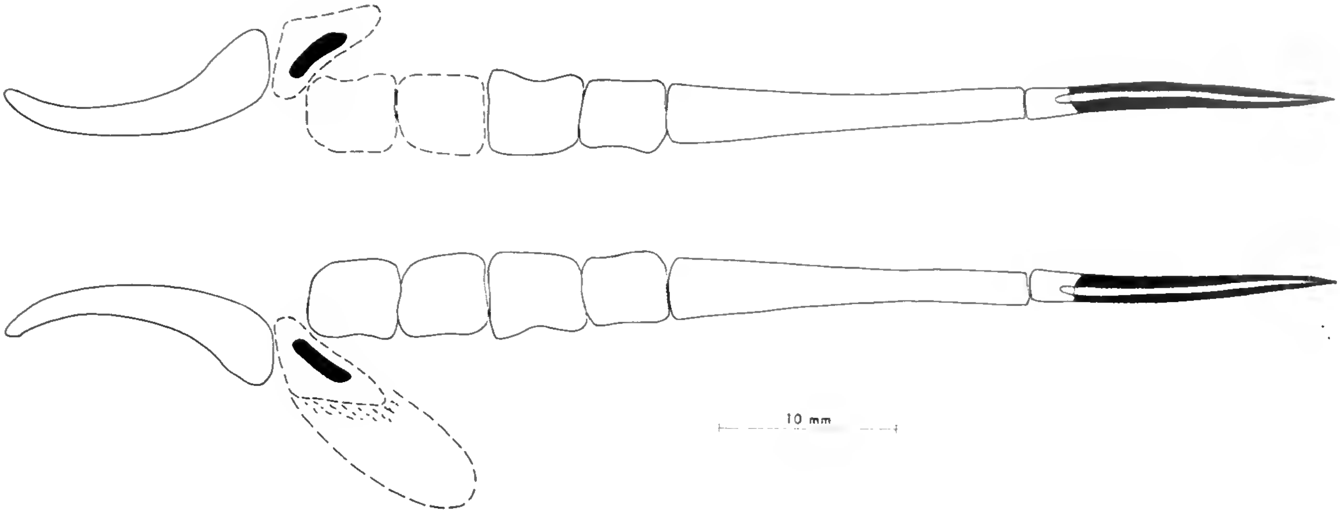

FIG. 76. Reconstruction of the pelvic complex of *Iniopera richardsoni*, based on several specimens.

(fig. 78) but it must be remembered that no whole skeletons are known, hence the proportions of the parts to one another may not be entirely correct.

Since the questions as to the nature and function of the pouches remains unresolved (see above), it is not yet possible to place this animal meaningfully into the flotant environment (Zangerl and Richardson, 1963) which it inhabited, along with all other iniopterygians.

FOOD:

To judge by the dentition this animal was probably able to avail itself of a variety of foods besides crustaceans such as *Concavicaris sinuata* which apparently was in plentiful supply in the flotant environment. The fact that the tooth whorls and mouth plates tend to be worn does not necessarily indicate that this fish ate hard-shelled prey; more likely it fed on whatever foods happened to be available (as do modern Eagle rays) and this almost certainly included leftovers produced by the large numbers of sharks that inhabited this environment, namely partly eaten sharks, iniopterygians, palaeoniscoids, and acanthodians. The calcified skeletons of these fishes might have provided the abrasive that ground down the tooth whorls and mouthplates of *Iniopera*. Since the bottom mud of the flotant environment was probably toxic (H_2S), it contained no infauna and hence none of the inhabitants of this habitat can be assumed to have been bottom feeders.

FIG. 77. Photograph of dermal denticles ("snowflakes") of *Iniopera richardsoni*, PF6535.

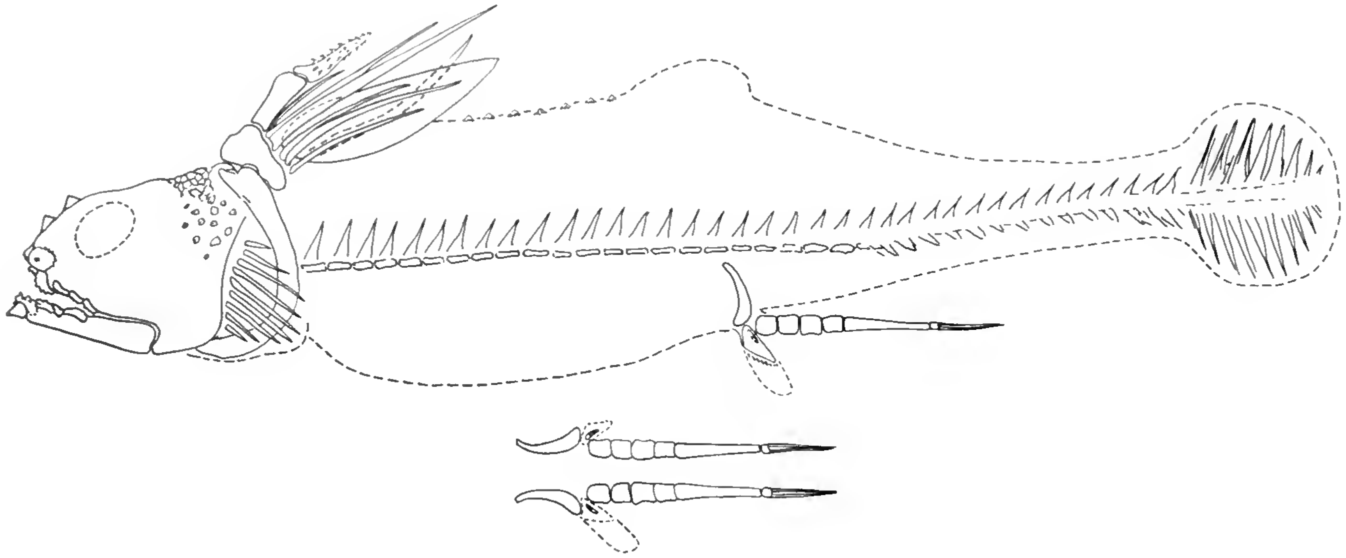

FIG. 78. Tentative reconstruction of the skeleton of *Iniopera richardsoni* in lateral view. The proportions of the different parts of the skeleton are only approximately correct.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE:

Iniopera richardsoni is a very common member of the Mecca fauna of the Illinois basin and is not at all rare in the western localities. For reasons not apparent, the majority of the western specimens are juveniles and so far no specimens have been found in the western localities that show the pouches. The most likely reason for this is the extreme rarity of adult skeletons in those localities. *I. richardsoni* has been collected in most of the localities shown on Figure 1 and may be expected in any black shale horizon in which iniopterygians occur.

Genus **Inioxyele**[1], gen. nov.

Characterization.—Iniopterygians with sharp-toothed dentition, consisting in the lower jaw of a symphyseal and four pairs of whorls; the "canine" whorl being the second from the symphyseal whorl. Roof and floor plates of the mouth cavity present (but their shapes remain to be determined). One double tenacular hook on each side, located on the basipterygium. Each clasper consists of an elongated proximal element, a series of about four short pieces and an elongated terminal rod that tapers to a point. Tiny clasper hooks present at distal end of clasper apparatus.

Type species.—*Inioxyele whitei*, n. sp.

Inioxyele whitei,[2] n. sp.

Type.—FMNH PF6651, ♂, large portion of a skeleton divided on plate and counterplate, lacking the tail and much of the vertebral column.

Horizon and locality.—Queen Hill shale, Lecompton formation, Shawnee group, Virgil series, Stephanian A, Pennsylvanian

Ace Hill Quarry, Plattsmouth, Nebraska. Collected by W. D. White of Omaha, Nebraska

Additional material.—The present collection of iniopterygian material contains a considerable number of specimens either of very young individuals, or of badly disarranged partial skeletons some of which may well belong to this species. At this stage of our knowledge of the iniopterygians, however, it is not possible to identify with confidence any of these specimens to the species presently recognized.

Characterization.—As for the genus.

Description.—Unfortunately, the description has to be based on one individual, the holotype (fig. 79). This skeleton shows a number of features of the dentition and the clasper mechanism, sufficiently distinctive to rule out the possibility of its being an abnormal individual of one of the other species here defined. We believe that additional specimens will show that this form is as distinctive as are the other species here described.

As is most often the case with specimens from the black shales, this individual was discovered by splitting a piece of shale, and, as also happens most often, the split divided the skeleton on plate and counterplate, making it very difficult to study. The tooth whorls and the mouth plates were torn apart, but fortunately the tooth whorls of the lower jaw, though somewhat broken, display the original relationships to one another (fig. 80). The tooth whorls are provided with well-separated and sharply pointed tooth crowns as in *Sibyrhynchus;* the "canine" whorl is the second whorl from the symphyseal one, not the third, as in *Sibyrhynchus*. Also there is a very considerable size difference

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[1] From *inion*=nape, and *xyele*=rasp.

[2] The species is named after Mr. W. D. White who is a most indefatigable collector of iniopterygians and other fossils in the black shale localities around Omaha, Nebraska.

Fig. 79. *Inioxyele whitei*, PF6651 (holotype). Camera lucida drawing.

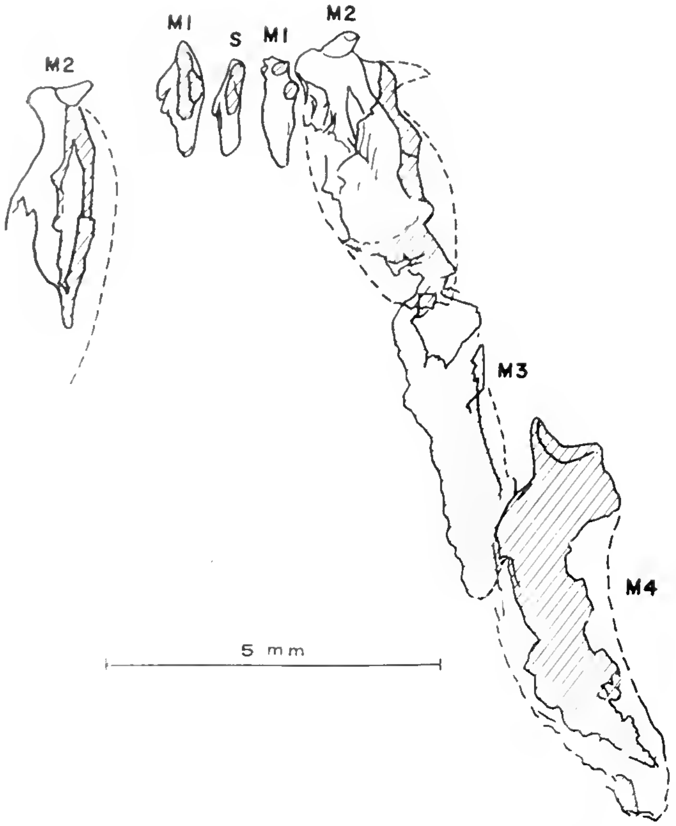

FIG. 80. Camera lucida drawing of the dentition as seen on the plate. *Inioxyele whitei*, PF6651 (holotype).

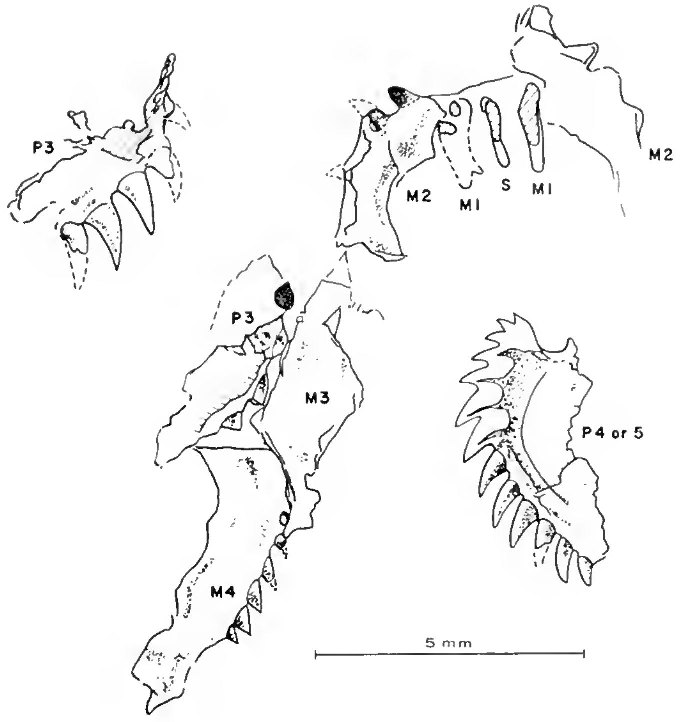

FIG. 81. Camera lucida drawing of the dentition as seen on the counterplate. *Inioxyele whitei*, PF6651 (holotype).

between M-1 and the "canine" M-2, a difference that is much less pronounced between M-2 and the "canine" M-3 of *Sibyrhynchus* (fig. 49). The dentition of the lower jaw of *Inioxyele whitei* consists of a symphyseal whorl and four pairs of whorls. Unfortunately, very little can be said about the tooth crowns, since most of them are broken off (fig. 80). On the counterplate (fig. 81), in addition to parts of the lower jaw dentition, there are a number of tooth whorls of the upper dentition. These whorls are not preserved *in situ* and their identification as to their position within the dentition is thus somewhat questionable. The whorl with the largest teeth, in the upper left corner of the illustration, is probably the "canine;" its mate (with broken tooth crowns) lies nearby.

The isolated whorl with 13 tooth crowns showing is either P-4 or P-5, P-4 being the more likely because of the notable curvature of this whorl. If the above interpretations are correct the dentition of *Inioxyele whitei* (fig. 82) differs considerably from that of *Sibyrhynchus denisoni*, even though the individual tooth whorls are very similar.

The mouth cavity of this fish was armored by plates much as in *Sibyrhynchus* and *Iniopera*, but at this time their shapes cannot be made out, nor their arrangement on the floor or the roof of the mouth cavity.

The pectoral fins of the male had a somewhat enlarged first ray which bore 60–80 rasp hooks with large bases that diminish in size distad. These rasp hooks are very similar to those of *Promexyele* (fig. 37). The vertebral column has almost completely disintegrated; what is visible suggests that the column was organized much as in other iniopterygians.

The pelvic elements are slender, slightly curved, distally somewhat expanded cartilages (fig. 79). Attached to them were the triangular basipterygia of the pelvic fins. Tenacular hooks, single or double on each side, apparently were located on the basipterygia (fig. 83).

The clasper mechanism consists on each side of a longish proximal rod, followed by four or five short segments and ends in another elongated distally tapering

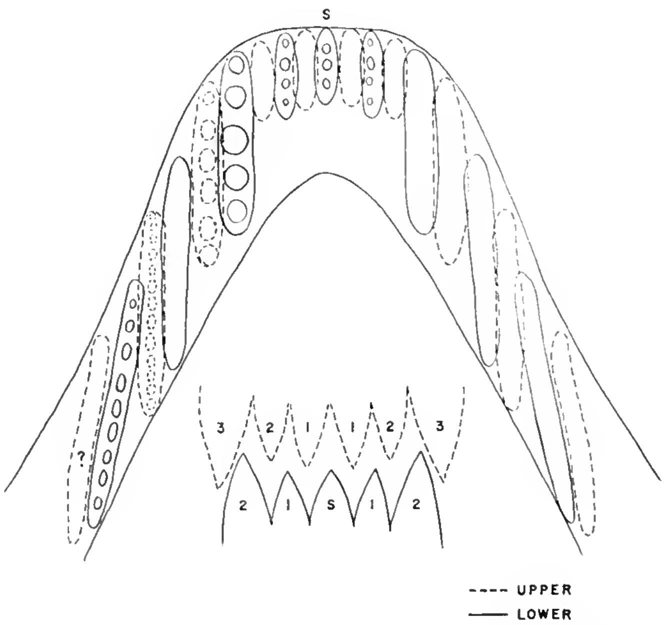

FIG. 82. Reconstruction of the dentition of *Inioxyele whitei*.

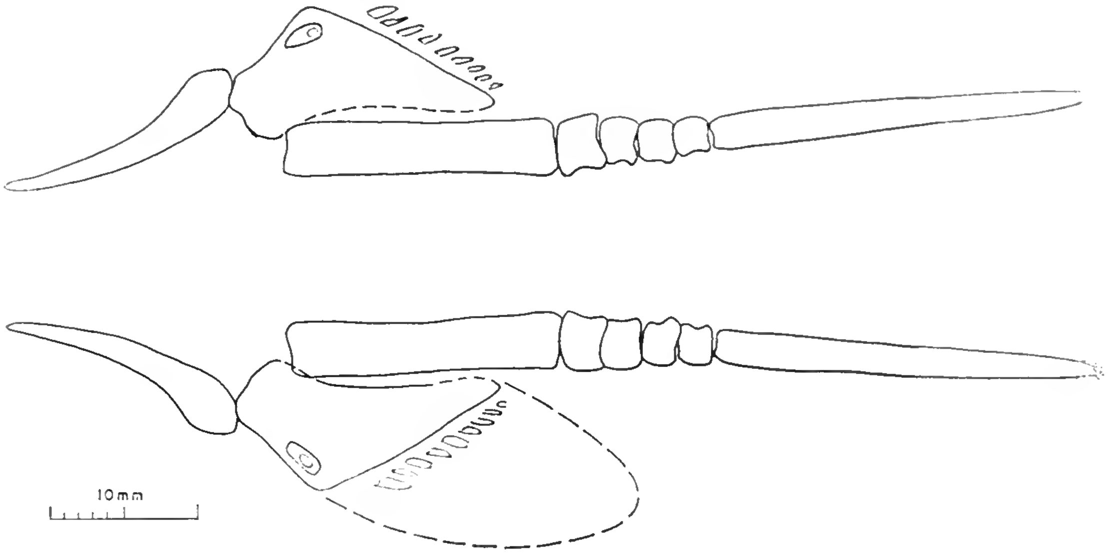

FIG. 83. Reconstruction of the pelvic complex of the male of *Iniox yele whitei*.

cartilage rod (fig. 79, 83). The very tip of the latter may or may not have consisted of a sclerotized tissue similar to that in *Iniopera* (p. 56). Near one of these terminal clasper pieces there is a small accumulation of very curious, tiny denticles, no two of which appear to be alike (fig. 79). We interpret these as terminal clasper hooks that have the shape of tiny hands with variable numbers of fingers (fig. 79).

COMPARATIVE ANATOMICAL AND PHYLOGENETIC SIGNIFICANCE OF THE INIOPTERYGIA

The seven species of fossil fishes described above conform in their structural organization to a mutual plan: the skeletons consist of calcified cartilage; the skull is unquestionably autostylic; the pectoral fins are enlarged and attached to the shoulder girdle near the dorsal end, thus extending from the body near the "nape" of the neck; the gill region was evidently covered by an opercular flap; the tail region is slender and the tail fin is more or less circular in side view; the males have species-characteristic, elaborate clasper mechanisms and tenacular hooks ventral to the pelvic cartilages or on the basipterygia of the pelvic fins, and a variety of denticles attached to the enlarged first pectoral fin ray; the dentition varies from simple, conical denticles arranged in labio-lingual tooth families, to tooth whorls, fusions of the elements of single tooth families, to complex dental plates probably involving the fusion of several adjacent tooth whorls; the mouth cavity, both roof and floor, may be armored with plates formed by the fusion of patches of mucous membrane denticles; the skin is usually naked, devoid of dermal denticles, except about the snout, and, in one genus, where there are patches of modified dermal denticles about the head and individual ones in the region of the thorax; the spiral membrane inside of the spiral intestine performed at least 14 turns (observed in *Iniopteryx rushlaui* only).

This combination of features leaves no doubt but that their bearers are chondrichthyans. Moreover, the character assemblage includes typical aspects of both chondrichthyan subclasses, the Elasmobranchii and the (chimeraeroid) Holocephali[1] as follows:

Elasmobranch structural affinites: the dentition in the more generalized genera; the large number of turns of the spiral membrane of the spiral intestine; the terminal mouth opening; the cartilaginous finrays of the pectoral and tail fins which extend to the margins of these fins (the last two characters being typical of Paleozoic elasmobranchs).

Chimaeroid structural affinities: the autostylic jaw suspension; a cartilage ray-supported opercular flap; the slender tail (though not the tail fin); the presence of tenacular hooks; the general nakedness of the skin; the tendency toward dental fusions[2]; the elaborate clasper mechanisms in males; the overall bizarre appearance of the animals.

The combination of elasmobranch and chimaeroid features makes the Iniopterygia structural intermediates between the two compared groups, not, however, phylogenetic intermediates.

Both the iniopterygians and the chimaeroid holocephalians are structurally compact and clearly circumscribed groups. The morphological distinctions between them represent different structural solutions to similar problems, as shown in Table 1.

Table 1 suggests a sister group relationship, *sensu* Hennig (1966), between the two groups, a conclusion that necessitates the postulation that relatives of the chimaeroid holocephalians existed in Pennsylvanian time. The question as to whether any of the known Paleozoic chondrichthyans could possibly be regarded as relatives of the chimaeroids was most recently analyzed by Patterson (1965). His arguments strongly pointed toward *Helodus simplex* Agassiz, though a number of features of this fish seemed to militate against such an assignment—for example, the selachian type of dentition with numerous tooth families along the jaws and several teeth in each family; the presence of a dorsal spine of peculiar microscopic anatomy (but with one chimaeroid structural detail); and the absence of dermal armor on the head.

With the discovery of the iniopterygians the question of the systematic position of *Helodus* becomes once more acute. Clearly, the shark-like dentition of this fish is no longer an obstacle to its being considered as a primitive chimaeroid, nor is the absence of dermal head armor. The matter of the dorsal spine is somewhat inconclusive inasmuch as the section (Patterson, 1965, pl. 22, fig. 48) was probably ground from the lower part of the spine where it accomodated the basal cartilage of the fin, while the section through the *Chimaera* sp. spine (loc. cit., fig. 45) probably was made from a more distal portion of the structure. Since the microscopic anatomy of chondrichthyan fin spines is notably com-

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[1] The suborder Chimaeroidei, as here understood, includes only the families Squalorajidae, Myriacanthidae, Chimaeropsidae, Acanthorhinidae, Chimaeridae, Rhinochimaeridae, and Callorhynchidae.

[2] The complex microscopic anatomy of the dental plates of chimaeroids suggests that these structures are the result of fusion of more primitive dental elements, though embryological work has furnished no hint of such a history.

TABLE 1.

Iniopterygia	Chimaeroid Holocephalia
Paired, denticulated, pectoral fin rasps (claspers)	Unpaired, denticulated head claspers
Mucous membrane denticles in mouth cavity with tendency toward fusion into plates	No mucous membrane denticles
Sensory canals probably not lined with dermal denticles	Sensory canals lined with dermal denticles
Trend toward fusion of dentition teeth belonging to tooth families to form tooth whorls, and of adjacent tooth whorls	Mode of fusion of dentition teeth to form dental plates not known, but almost certainly different from that of iniopterygians
A single dorsal fin without a spine	Two dorsal fins, first with a spine
Tail fin circular in side view	Tail fin tapering to a point
No fusion of the anterior vertebral arches	Fusion of anterior vertebral arches (synarcual) in connection with the anchoring to the dorsal spine

plex[1] and not yet adequately understood, the differences noted by Patterson do not seem to weigh heavily at this time. By contrast, the similarities between the chimaeroid skeleton and that of *Helodus* as summarized by Patterson (1965) are most impressive, and we can find no convincing argument that would preclude the assignment of *Helodus* to the order Chimerida.

Patterson (1965) included among the Chimaeriformes not only the chimaeroids proper, but also the menaspoids, represented by the Permian genus *Menaspis* and the Carboniferous *Deltoptychius*. Bendix-Almgreen (1971) re-examined the best-preserved skeletons of *Menaspis* and came to a different interpretation of its morphology than did Patterson (1965, 1968). As a consequence of this, Bendix-Almgreen has ruled out the possibility of a close phylogenetic relationship between *Menaspis* and the chimaeroids. In view of the fact that *Menapsis* has nothing in common with the iniopterygians, we are inclined to agree with the views of Bendix-Almgreen.

Among the Holocephali Patterson (1965) not only included the Chimaeriformes (including the menaspoids and, *incertae sedis*, the cochliodonts), but, in addition, a host of groups that are very poorly known at present: the copodonts, the psammodonts, the petalodonts, as well as the helodontids, the edestids, and the chondrenchelyids.

There is no gain in speculating on the possible affinities of the above groups that are known only from teeth. The edestids, to judge from such genera as *Fadenia*, *Agassizodus*[2], and *Ornithoprion*, are specialized elasmobranchs with a tendency toward reduction (not demonstrated in *Fadenia*) of the palatoquadrates.

Chondrenchelys problematica from the lower Carboniferous of Scotland stands at the present almost completely isolated among chondrichthyans. The differentiation of its median fins has no parallel among any other forms, and its biserial pectoral fins occur only in pleuracanth sharks, none of which have large, flat tooth plates. The skull is thought to be autostylic, since no separate palatoquadrate could be detected. However, there are not many specimens and no isolated neurocrania to establish this point beyond doubt.[3] Only the vertebral column with its rings, presumably calcifications in the sheath of the notochord, resembles the chimaeroids. In the absence of any other chimaeroid characters, we prefer to place *Chondrenchelys*, *incertae sedis*, among the elasmobranchs.

The present analysis thus results in the conclusion that the subclass Holocephali contains only two orders, the Iniopterygia as defined above, and the Chimaerida with the suborders Helodontoidei and Chimaeroidei.

The question of the phylogenetic relationships of the holocephalians not only occupied Patterson (1965), but more recently Stahl (1967) who approached the problem primarily (though not exclusively) with morphological arguments based on modern chimaeroids and elasmobranchs. Throughout the analysis Stahl carefully notes the fact that the numerous similarities that exist in the anatomical makeup of elasmobranchs and chimaeroids may not be the result of the descent of one group from the other but rather a reflection of primitive features inherited by both groups from their respective ancestors. In the case of soft anatomy, questions of this sort can, unfortunately, rarely be resolved by the fossil record. Stahl makes the valid point, however,

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[1] See, for example, Peyer (1946) and Markert (1896) where the complexity of the developing *Acanthias* spine is further complicated by the author's misorientation of his sections. Compare Markert, 1896, pl. 49, fig. 28, where the anterior face of the spine (right side of picture) is erroneously taken as the posterior side thus confusing some of the structures, with pl. 48, fig. 21, where the orientation is correct.

[2] Much material of this genus is at hand, but not yet described.

[3] Skulls consisting of prismatic, calcified cartilage rarely show useful anatomical detail after collapse due to bacterial degradation prior to fossilization.

that the anatomical similarities between extant holocephalians and selachians set both groups apart from the bony fishes and suggests that they shared a common ancestor among placoderm or even preplacoderm fishes. In the end Stahl concludes that while "the specific group of placoderms from which sharks originated is unknown, the ptyctodonts may represent the root of the holocephalian line."

The discovery of the iniopterygians sheds further light on this question. For one thing, the dentition is typically elasmobranch in *Iniopteryx* and *Promexyele* and a dentition of this sort is not known among placoderms. Iniopterygians also lack bony armor about the head, and bone, as a tissue, is only associated with the bases of denticles, much as in the shark *Ornithoprion*. These features alone make it unnecessary to search for an ancestor of the holocephalians among the placoderms.

The earliest evidence of elasmobranchs in the fossil record, about the middle of the Devonian period, consists of compound scales, in principle similar to the compound scales of later Paleozoic forms. The earliest elasmobranchs therefore appear to have already displayed the characteristic selachian denticulation of the skin which in later Paleozoic forms consisted of simple lepidomoria on the ventral parts of the skin and of progressively more complex aggregations of lepidomoria (complex scales) from the flanks to the dorsum of the hide. Since differentiated shark teeth are not associated with the earliest scales, it seems probable that the stomodaeum was covered with small, simple, conical denticles, not much different from the shagreen of the underside of the animal. This clearly seems to be close to the primitive condition for the chondrichthyans whose ancestors, in all likelihood, never possessed heavy, dermal armor, but instead had an even spread of lepidomorial denticles over the entire surface of the skin and the stomodaeum. Both the elasmobranchs and the holocephalians (as here defined: Iniopterygia plus Chimaerida) probably evolved from such a generalized chondrichthyan stock, and represent at the present state of our knowledge, sister groups, *sensu* Hennig (1966).

The systematic grouping of the chondrichthyans as suggested by the new evidence may thus be summarized as follows:

- Class Chondrichthyes
  - Subclass Elasmobranchii
  - Subclass Holocephali
    - Order Iniopterygia
      - Family Iniopterygidae
      - Family Sibyrhynchidae
    - Order Chimaerida
      - Suborder Helodontoidei
        - Family Helodontidae
      - Suborder Chimaeroidei
        - Family Squalorajidae
        - Family Myriacanthidae
        - Family Chimaeropsidae
        - Family Acanthorhinidae
        - Family Chimaeridae
        - Family Rhinochimaeridae
        - Family Callorhynchidae

In view of the discovery, in recent years, of new Paleozoic fish faunas that include much unstudied chondrichthyan material, we may confidently look forward to a much better understanding of the abovementioned relationships as these new materials are described. Moreover, the fact that it is still possible to discover whole groups of vertebrates that have escaped our notice should once again focus attention on the probability that the fossil record is far from adequately known.

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