Geology

DEVONIAN LUNGFISHES
WYOMING, UTAH, AND IDAHO

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EARLY DEVONIAN LUNGFISHES

FROM WYOMING, UTAH, AND IDAHO

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I. A Lungfish from the Beartooth Butte Formation
of Wyoming

Fragments of Early Devonian lungfishes have been collected on a number of Field Museum expeditions, some as early as 1949. With the exception of a few scales, plates, and a single tooth plate from the Water Canyon formation of Utah and Idaho, all of this material has come from two localities in Wyoming. They are: 1) Beartooth Butte in Park County; and 2) Cottonwood Canyon, east of Lovell, NE $\frac{1}{4}$, sec. 4, T 56 N, R 93W, Bighorn County. The first is the type locality of the Beartooth Butte formation, and has previously yielded plants, a few eurypterids, and many fishes, including a poorly preserved and indeterminable lungfish specimen which was doubtfully listed by Bryant (1932, p. 254) as a skull of *Dipterus* (Princeton University 13503). A variable series of sediments at the Cottonwood Canyon locality has also been referred to the Beartooth Butte formation by Sandberg (1961, p. 1305). It contains a considerable flora and fauna, similar to those of Beartooth Butte, but as yet undescribed except for *Cardipeltis* (Denison, 1966). The rocks at these two localities are believed to be approximately the same age, and have been correlated (Denison, 1958, p. 500; 1964, p. 451) with the Early or perhaps Middle Siegenian of the western European section. If this is correct, the Beartooth Butte formation lungfishes are the earliest ones known, predating the German *Dipnorhynchus lehmanni* from the Late Siegenian Hunsrückschiefer (Lehmann and Westoll, 1952), and *D. sussmilchi* from the Emsian or Late Siegenian of Australia (Philip and Pedder, 1964). A new lungfish from northern Canada, *Melanognathus*, recently described by Jarvik (1967, pp. 167–170), is doubtfully dated as late Lower Devonian; however, since it is associated with paleoniscoid scales, it is very probably younger.

It is interesting and somewhat surprising that both *Dipnorhynchus lehmanni* and *D. sussmilchi* (Hills, 1958, pp. 87–88) occur in undoubted marine rocks. This is not true of the Beartooth Butte lungfish, since at Beartooth Butte and Cottonwood Canyon definitely marine invertebrates are absent, and deposition is in channels

cut into the underlying Ordovician limestones. On the other hand, it is not possible to conclude definitely that these are deposits of freshwater streams. One reason for this is that in Utah many of the same vertebrates occur in the Water Canyon formation, which is a widespread and at least in part a marine deposit. Dorf (1934, pp. 735–736) concluded that the channel-fill at Beartooth Butte was formed in fresh or brackish water under estuarine conditions in a drowned river valley. Several years ago I concluded (Denison, 1956, p. 414) that it might have been formed in the arm of a marine bay. Sandberg (1961, p. 1308) suggested that the Beartooth Butte formation was deposited in many different continental and shallow-water, marginal marine environments, the latter related to a sea that invaded Wyoming from the west. When the study of the fauna and flora of Cottonwood Canyon is completed, it may be possible to come to more definite paleoecological conclusions. All that can be said now is that the varied lithology (Denison, 1966, p. 90) indicates deposition in a great variety of conditions, and it is possible that some were on the margins of the sea and that others were in freshwater streams and pools.

The fragmentary material from the Water Canyon formation will be described at the end of this paper (p. 407). All of the identifiable specimens of lungfishes from the Beartooth Butte formation are referred to a single species, which is distinguished from previously described Dipnoi as the new genus *Uranolophus*. All material is in Field Museum collections, except for one specimen in the collection of Princeton University.

Uranolophus[1] new genus

Type-species.—*Uranolophus wyomingensis*, new species.

Diagnosis.—A pineal foramen is absent. There is a single bone D in the pineal region of the skull roof. The prepineal region of the skull roof is relatively short (prepineal length/total length of skull roof is 0.35). The supratemporal region of the skull roof is relatively long (bones X - Y_1 - Y_2 occupy about one-half of the total length of the skull roof). Pterygoid and prearticular tooth plates are absent; the margin of each pterygoid and prearticular is crowned with a "tooth ridge," which is a continuous, irregular crest of dentine with numerous side ridges.
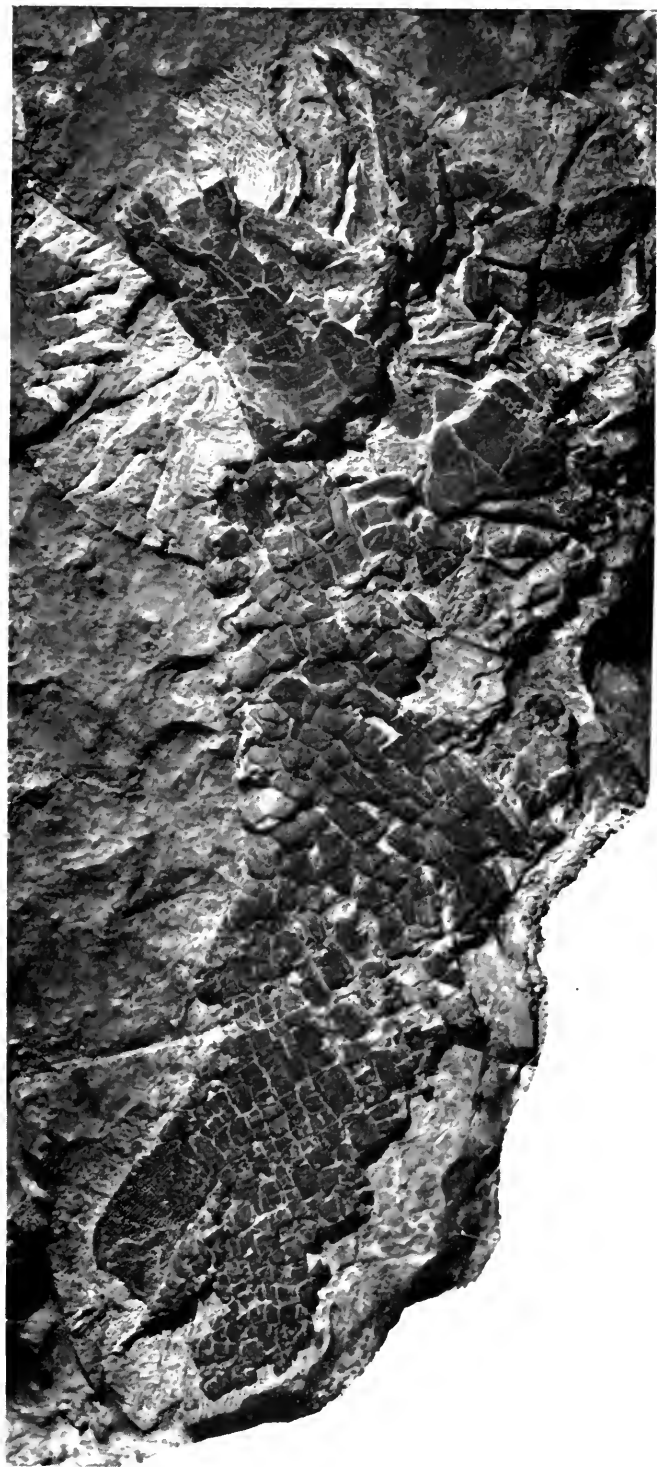
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[1] From ουρανος, palate; and λοφος, ridge.

FIG. 1. Largely articulated type specimen of *Uranolophus wyomingensis*, n. sp., PF 3874 (× about 1·2).

Uranolophus wyomingensis new species

Type.—PF 3874, a largely articulated fish lacking the posterior and ventral portions of the body (figs. 1, 2, 4, 19, 21), from the Early Devonian, Beartooth Butte formation, Cottonwood Canyon, east of Lovell, Bighorn County, Wyoming.

Referred specimens.—From the Cottonwood Canyon locality: incomplete skull and jaws, PF 3795; skulls and partial skulls, PF 3792 (figs. 10, 15C–D), 3794, 3805 (figs. 6, 8, 15A–B), 3816 (fig. 5), 3817; snouts, PF 3843, 3847–8, 3860, 3868 (fig. 7); palates, PF 3793 (fig. 9A), 3796 (fig. 9B), 3841; pterygoids, PF 3801, 3803, 3807, 3844, 3867, 5524; operculars, PF 3833–5 (fig. 11A), 3839 (fig. 11B), 3852, 3870; probable suboperculars, PF 3836 (fig. 11C), 3837, 3840, 5518, 5522; gulars PF 3838 (fig. 11F), 3866 (fig. 11E), 5519; ceratohyals, PF 5514 (fig. 16), 5520; lower jaws, PF 3797 (fig. 13A), PF 3798 (figs. 13B, 14A), 3804, 3808, 3845, 3849 (fig. 22B), 3850, 3855, 3858, 3861, 3863, 3869, 5551; prearticulars, PF 3802, 3857, 3864 (fig. 15E); associated lower jaws, opercular, subopercular, ceratohyal, and scales, PF 3862 (figs. 11D, 20F); cleithra and clavicles, PF 3851 (fig. 17A), 5364; cleithra, PF 3846 (fig. 17B), PF 3856 (fig. 17C), 3859, 4333; ?interclavicle, PF 3865 (fig. 17D); flank scales, PF 5542, 5543, 5547 (fig. 20C), 5548 (fig. 20B), 5550; posterior flank scales, PF 5541 (figs. 24–25); median dorsal scales, PF 5544–5 (figs. 20D–E), 5549; various associated scales, PF 5546 (fig. 20A).

From Beartooth Butte, Park County, Wyoming: skull, PF 1427 (fig. 3A); lower jaws, PF 3318; associated scales, PF 3319; flank scales, PF 140, 275, 278–280; median dorsal scale, PF 5536; also in the Princeton University collection an impression of an operculum, PU 13658, originally figured by Ruedemann (1934, p. 3) as a coxal joint of *Pterygotus*.

Diagnosis.—As for genus.

Discussion.—*Uranolophus* is similar in many respects to the typical *Dipnorhynchus* (*D. sussmilchi*), but differs strikingly in the development of its "teeth." This in itself would appear to be adequate to distinguish it generically, but is reinforced by the consistent absence of a pineal foramen, and by proportional differences of evolutionary significance. The generic affinities of *Dipnorhynchus lehmanni* are uncertain; in its cranial roof it resembles *D. sussmilchi*, but its teeth, though poorly known, appear to be quite differently developed.

Dermal bones of the cranial roof.—The nomenclature of the dermal bones of the dipnoan skull roof has been discussed recently at some

FIG. 2. Skull and lower jaws of type specimen of *Uranolophus wyomingensis*, n. sp., PF 3874 ($\times$ 9/10).

length by White (1965, pp. 7–31), who uses a modification of the alphabetical notation introduced by Forster–Cooper in 1937 for *Dipterus valenciennesi*. In this paper White's notation for *Dipterus* will be followed with minor exceptions, of which the most important is that the bone he labels I_2 is called simply I. White reasoned that there is evidence that there was once an I_1 behind I_2, and indeed it is occasionally preserved in *Dipterus* and *Rhinodipterus*. But this bone lay in the transverse extrascapular series and would better be called H than I (though this is not the H of Forster–Cooper nor of Westoll's 1949 review).
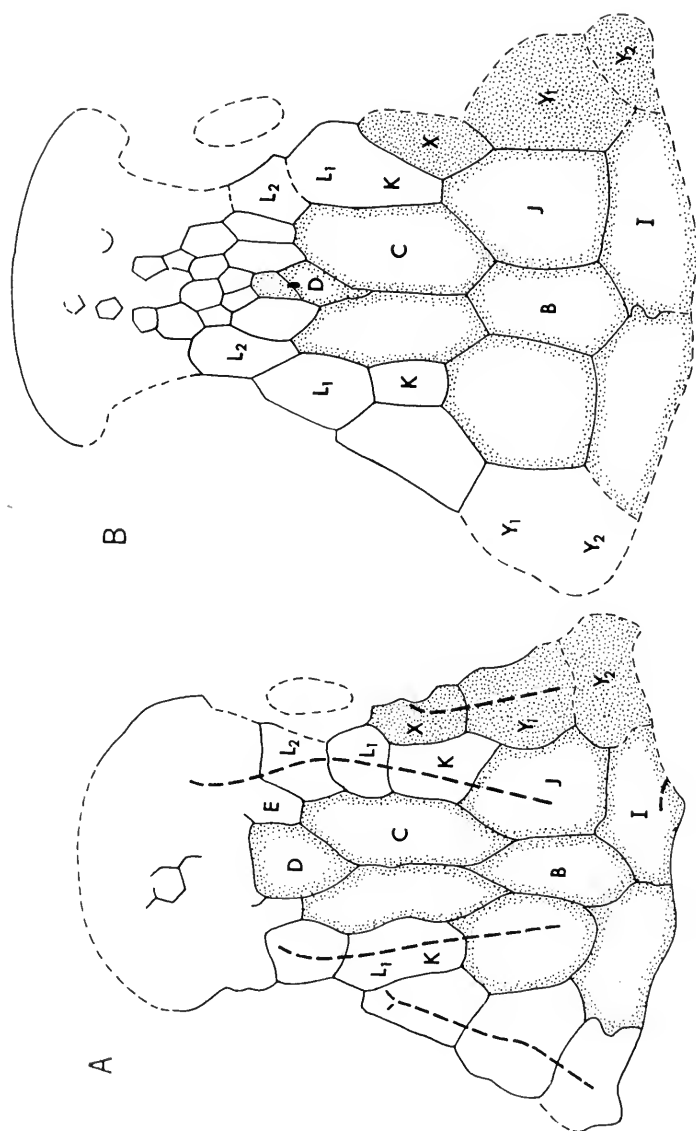
Fig. 3. Restoration of cranial roofs of early lungfishes, all enlarged so that the distance from the pineal opening or the center of bone D to the posterior end of the cranial roof is the same. Supratemporal bones solidly stippled, bones of posterior triangle stippled on margins. The approximate position of the orbit is indicated on the right. A, *Uranolophus wyomingensis*, n. sp., based on PF 1427; B, *Dipnorhynchus lehmanni*, modified from Lehmann and Westoll (1952).
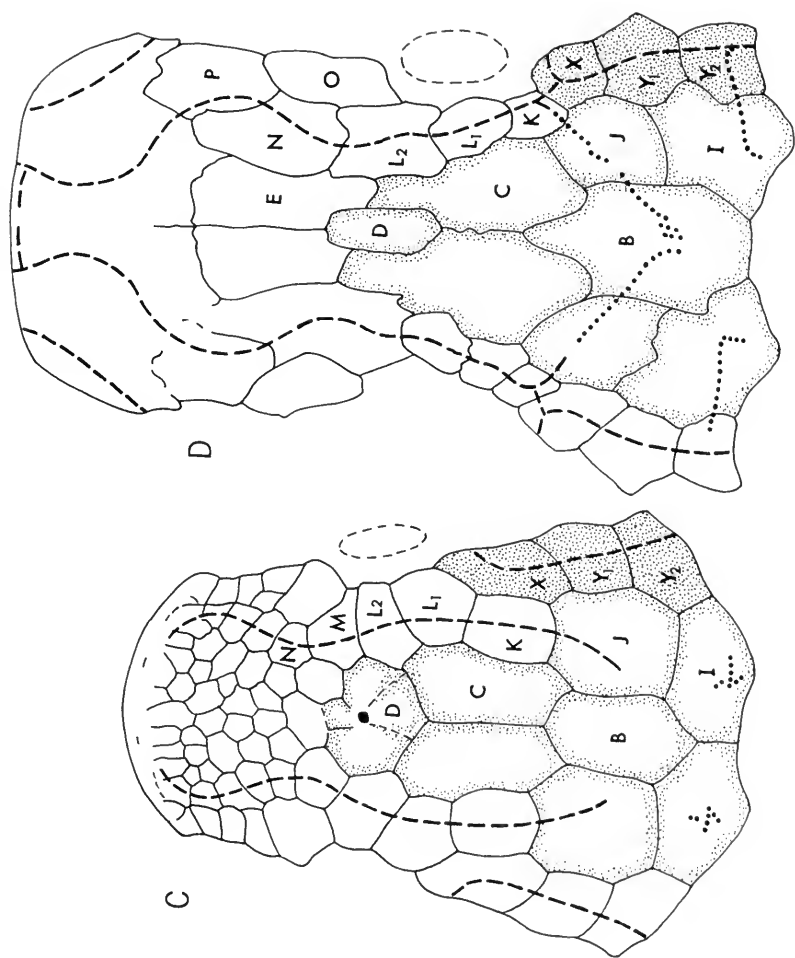
Fig. 3. (continued). C, *Dipnorhynchus sussmilchi*, from Campbell (1965) and Hills (1941); D, *Dipterus valenciennesi*, modified from White (1965).

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Those who have compared the skull of *Dipnorhynchus* with that of *Dipterus* have come to varied conclusions regarding the homologies of the important cranial roofing bones. My own interpretation of *Dipnorhynchus* and *Uranolophus* (fig. 3) differs in details or in important respects from earlier ones. It is based fundamentally on the great similarity in pattern between the eight bones forming a triangular area in the relatively stable postero-median part of the skull roof in these three genera. The bone pattern differs only in that B in *Dipterus* has pushed back between I–I to reach the posterior margin of the skull roof. The lateral-line system differs only in that the posterior end of the supraorbital canal of *Dipnorhynchus* and *Uranolophus* has become a pit line in *Dipterus* and has extended postero-medially onto B. According to this interpretation, the extrascapular series, Z–A–Z (or perhaps, Z–H–A–H–Z), was loosely attached to the posterior edge of the skull roof in *Dipterus*, where it is sometimes found, and in *Dipnorhynchus* and *Uranolophus*, where it has not yet been discovered.

In the interpretation favored by White (1965, fig. 33; 1966, fig. 4), the bones at the posterior edge of the skull roof of *Dipnorhynchus* are a distinct series (β–a–a–β), lost in *Dipterus* and in other lungfishes. This hypothetical series of bones introduces an unnecessary complication into an otherwise simple picture. A second interpretation suggested by White (1965, fig. 32) identifies as I–I the bones that are here labelled J–J. This makes it necessary to homologize the paired bones at the posterior margin of the skull with A–A, which is unlikely because A is a loosely attached median element in *Dipterus*. Westoll (1949, p. 141) identified the bones in *Dipnorhynchus* here called C–C as "B_2–B_2." This homology was based on the spatial relations of "B_2–B_2" to the lateral-line bones on either side, but it has little validity because Westoll's identifications of these lateral-line bones are, in my opinion, incorrect. Campbell (1965) used Westoll's homologies of *Dipnorhynchus* cranial bones, but implied reservations as to their acceptance. The homolgies of Hills (1941, pp. 50–54) are difficult to understand because he makes his comparisons with osteolepids rather than directly with *Dipterus*, but as far as the posterior triangle under discussion is concerned, his homologies are apparently the same as my own. Romer's (1936, fig. 1A) homologies in this area of the skull are the same as my own.

If one accepts the homologies of I–I, B, J–J, C–C, and D, as here proposed, the lateral bones of the posterior half of the skull roof are easily identified. The more medial series of lateral-line bones, J–K–

L_1–L_2, have exactly the same relations to B and C in *Dipterus, Dipnorhynchus,* and *Uranolophus.* It is only in the variable more anterior members of this series that precise homologies cannot be attempted. The genera differ in that the posterior continuation of the supraorbital canal onto K and J of *Dipnorhynchus* and *Uranolophus* has become in part the anterior pit line of *Dipterus.* The lateral or supratemporal series of lateral-line bones shows differences, yet can be homologized simply. The bone at the postero-lateral corner of the skull roof is identified as Y_2 in all three genera. This implies that the extra-scapular bones (Z–A–Z), if evolved as distinct elements, lay behind the skull roof. Y_1 consistently overlies the fused otic process of the palato-quadrate. The bone in which the main lateral line canal turns down to become the infraorbital canal is identified as X. White (1965, figs. 20, 21, 23) has identified this as Y_1 in some specimens of *Dipterus,* but this homology is open to question. The position of this sensory canal is known definitely in *Dipterus valenciennesi* and *Uranolophus wyomingensis,* and its probable course is known in *Dipnorhynchus sussmilchi.* The Y_2–Y_1–X series, as so identified, is relatively long in *Uranolophus,* occupying nearly half of the total length of the cranial roof. This is presumably the primitive condition in lungfishes. In *Dipnorhynchus sussmilchi* and *D. lehmanni,* it occupies about 44 per cent of the cranial roof length, while in *Dipterus* this series is much shorter, a result, no doubt, of the reduction of the subjacent cheek region. In spite of this shortening, the relations of bones Y_2–Y_1–X to I–J–K remain much the same, though in *Dipterus* X no longer contacts I_1, and Y_2 no longer contacts J, as is usual in *Dipnorhynchus* and *Uranolophus.* One result of the shortening of the supratemporal part of the skull roof is that the supraorbital canal in K has approached the infraorbital canal in X, and a commisure has formed between them in *Dipterus.*

None of the previous students of *Dipnorhynchus* has come to similar conclusions regarding the homologies of the lateral series of lateral-line bones. Hills (1941, fig. 6) correctly identified X, but added an additional extrascapular bone at the postero-lateral corner of the skull roof, which modified his homologies of Y_2 and Y_1. Romer (1936, fig. 1A) followed Hills in adding an extra bone, and this led him to place the equivalent of X too far posteriorly. Westoll (*in* Lehmann and Westoll, 1952, fig. 5) and White (1965, figs. 32, 33) have, in my opinion, placed X too far forward, and, as a result, have misinterpreted the bones behind it in this series.

FIG. 4. Skull of type specimen of *Uranolophus wyomingensis*, n. sp., PF 3874 ($\times$ 3/2). *ar*, articulatory area for lower jaw; *co*, circumorbital or cheek plates; *ifc*, pores of infraorbital sensory canal; *ll*, pores of main lateral line; *occ*, pores of occipital commissure; *pl*, pit line; *pq*, palatoquadrate; *pr*, process on dorsal face of pterygoid; *pt*, pterygoid; *soc*, pores of supraorbital sensory canal; *tr*, tooth ridge.

As is usual in early lungfishes, there is considerable variation in the pattern of the cranial bones of *Dipnorhynchus* and *Uranolophus*. The following have been noted in the central and posterior parts of the skull roof:

C–C are partly fused in the type of *D. sussmilchi* and in one specimen of *Uranolophus wyomingensis* (PF 3795). This is known to occur in *Dipterus* also (Westoll, 1949, fig. 3E; White, 1965, fig. 7).

In *D. lehmanni* and in one specimen of *U. wyomingensis* (PF 1427, fig. 3A), K and L_1 are separate on one side, but represented by only one bone on the other. In *D. lehmanni* Y_1 and Y_2 are separate on the right, a single bone on the left. As shown by Parrington (1949)

FIG. 5. Incomplete cranial roof of *Uranolophus wyomingensis*, n. sp., PF 3816 (× 1), showing Westoll lines and areas of cosmine resorption (stippled).   Where dermal bones have been lost, the impressions of their inner surfaces show radiating lines.

and White (1965, p. 12) these variations may be interpreted as fusions, or as the loss of one bone and invasion by the other.   They are common in the lateral-line series of *Dipterus* (Westoll, 1949, p. 132).

In a number of specimens there are supernumerary bones, usually absent in other lungfishes; they may be interpreted as relics of an ancestral stage when the skull roof was covered by a mosaic of small bones.   In the L region of the lateral-line series of the type of *Dipnorhynchus sussmilchi* there are three bones on the left, and the usual two occupying the equivalent area on the right.   In the type specimen of *Uranolophus wyomingensis* (PF 3874, fig. 4) there are four

instead of three bones in the supratemporal series, two of which occupy about the same space as the usual Y_1. On the left side of a specimen of *U. wyomingensis* (PF 3816, fig. 5) J is represented by two bones lying side by side. A comparable situation has been recorded in a specimen of *Soederberghia* (Lehman, 1959, fig. 12) where there is a small bone medial to one J. Also, in *Dipterus* and *Scaumenacia* (Westoll, 1949, figs. 2B, 6B) J may be represented by two bones, one behind the other. Y_1 is represented by two bones lying side by side on the right side of the type of *D. sussmilchi*. Westoll (1949, p. 145, fig. 6D) found a similar situation in *Scaumenacia*, and considered the more lateral bone to be a "separate prespiracular bone."

There are variations in the mutual relations of bones. Thus Y_1 and I are not in contact in *D. sussmilchi* and on one side of three specimens of *U. wyomingensis* (PF 1427, fig. 3A; 3816, fig. 5; 3874, fig. 4). X and J do not contact in the type of *D. sussmilchi* and on one side of two specimens of *U. wyomingensis* (PF 1427, fig. 3A; 3874, fig. 4).

The differences mentioned above are clearly individual variations, but two other differences in the posterior triangle of the cranial roof are considered to be of generic significance. One is the absence in *Uranolophus wyomingensis* of a pineal foramen, which is present in *Dipnorhynchus*. The other is the presence in *U. wyomingensis* of a single and sometimes large D bone in the pineal region, while *D. lehmanni* (fig. 3B) has two bones in this area, and *D. sussmilchi* (fig. 3C) shows evidence of three or four.

The anterior part of the skull roof has little or no ossification in some Late Devonian and in known post-Devonian lungfishes. In *Dipterus valenciennesi* an ossified, cosmine-covered snout is usually absent in small specimens and is invariably present in large ones; according to White (1965, p. 7), this may have been because it formed only at a certain size or age. When it is present in *Dipterus*, it is always a single unit with no evidence of the mosaic of small, separate ossifications that are believed to have characterized the ancestral dipnoan (Westoll, 1949, fig. 10A). This mosaic is actually known in only three genera—one is the Upper Devonian *Soederberghia* (Lehman, 1959, figs. 2-4) where the anterior part of the skull roof is covered with a large but variable number of bones lacking any cosmine coating. The others are *Dipnorhynchus* and *Uranolophus* where separate ossifications are well displayed only in an occasional individual. One of the best is the specimen of *D. sussmilchi* described

by Campbell (1965, fig. 1) where there are about seven lateral-line bones on each side anterior to L_2, five or more marginal bones on each side, and 29 anamestic bones between the lateral-line bones (including the bones in the pineal area).   Only the thick, anterior mar-

FIG. 6.   Anterior part of skull of *Uranolophus wyomingensis*, n. sp., showing mosaic of small plates near snout, PF 3805 ($\times$ 1).

gin of the snout does not show subdivision into individual bones. One specimen of *Uranolophus wyomingensis* (PF 3805, fig. 6) has the entire anterior part of the skull roof (with the exception of a much-enlarged D) subdivided into what appear to be small distinct ossifications; here the subdivision extends even onto the anterior margin of the snout.   An isolated snout (PF 3868, fig. 7A) shows a similar tendency toward apparent subdivision along the rostral margin.   In
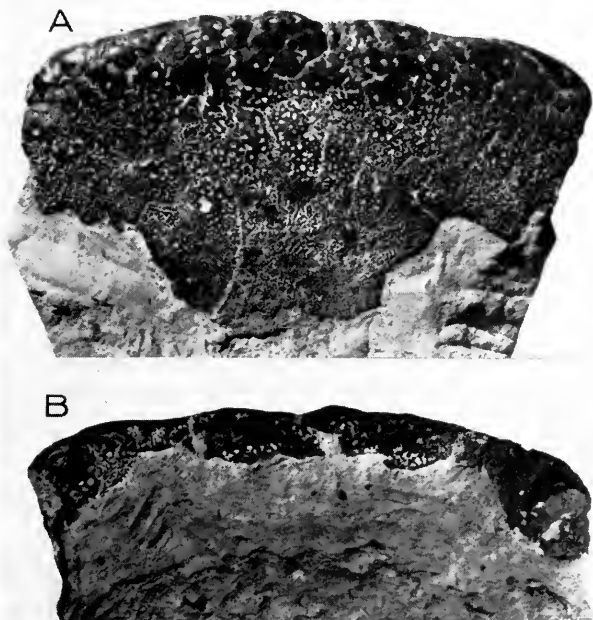
Fig. 7. Snout and upper lip of *Uranolophus wyomingensis*, n. sp., PF 3868 (× 1). A, dorsal view; B, ventral view.

other specimens of *Dipnorhynchus* the mosaic of small plates is poorly developed.   In the type of *D. sussmilchi* only the interorbital area shows individual ossifications.   In the type of *D. lehmanni* the central area anterior to the pineal opening shows about 15 small ossifications.   In other specimens of *Uranolophus wyomingensis* two, one, or no distinct ossifications are apparent.   The tendency toward subdivision of the snout is presumably a relic of the ancestral condition, but in *Dipnorhynchus* and *Uranolophus* it is so variably expressed that it is of little use as a systematic character.

Perhaps the most striking differences in the cranial roofs of *Dipnorhynchus*, *Uranolophus*, and *Dipterus* are those of proportions.   This is well shown by Figure 3 where the skulls are all drawn with the same post-pineal lengths (measured from the pineal opening or the center of bone D to the posterior edge of bones I in *Dipnorhynchus* and *Uranolophus* or bone B in *Dipterus*).   The most important differences are:

1. The prepineal part of the skull is very short in *Uranolophus*, slightly longer in *Dipnorhynchus*, and much longer in *Dipterus*.   The

prepineal length is about 35 per cent of the total skull length (excluding any extrascapular bones) in *Uranolophus wyomingensis*, 42 per cent in *Dipnorhynchus lehmanni*, and *D. sussmilchi*, while it is approximately 50 per cent in *Dipterus valenciennesi*. There is no suggestion in these genera that the growth of the snout is allometric, and that it became relatively longer in larger individuals, as has been shown to be the case in the long-snouted *Soederberghia* by Lehman (1959, pp. 35–37).

2. The postero-lateral or supratemporal part of the skull roof, including bones $X-Y_1-Y_2$, is long in *Uranolophus* and in *Dipnorhynchus*, and considerably shortened in *Dipterus*. The length of this series of bones is approximately half of the total skull length in *Uranolophus wyomingensis*, 44 per cent in *Dipnorhynchus lehmanni* and *D. sussmilchi*, and only one-third of the skull length in *Dipterus*. The shortening of these bones is related to the shortening of the cheek region.

3. The orbits lie anterior to midlength of the skull roof in *Uranolophus* and *Dipnorhynchus*, while they are behind midlength in *Dipterus*. This is related both to the shortening of the cheeks and the lengthening of the prepineal part of the skull.

Westoll (1949, p. 163) claimed that a shortening of the otic region of the neurocranium was a general evolutionary trend in Dipnoi, and specifically that the otic region was shorter in *Dipterus* than in *Dipnorhynchus*. However, though the otic region is known to be very short in *Dipterus* and *Chirodipterus* (Säve–Söderbergh, 1952, pp. 15–19), it is as yet unknown in *Uranolophus* or *Dipnorhynchus*, and its extent cannot be determined easily from the extent of the cranial roofing bones. In *Dipterus*, *Uranolophus*, and *Dipnorhynchus* the otic process of the palatoquadrate underlies Y_1, and indicates the position of the anterior part of the otic region to which it is fused. The position of Y_1 suggests that the otic region was very short in *Uranolophus* and *Dipnorhynchus*, also.

Ventral side of the skull.—The dermal shield of the ethmoidal region turns down at the snout, and then curves postero-ventrally to form the so-called "upper lip," which is developed in *Uranolophus* (figs. 7B, 8, *ul*) in much the same way as it is in *Dipnorhynchus, Dipterus, Rhinodipterus, Chirodipterus,* and *Ganorhynchus*. Medially, there is a relatively broad process which forms the anterior border of the mouth; this is divided in the middle in some specimens of *U. wyomingensis*. On either side of this process there is a deep notch which forms the anterior border of the anterior naris (fig. 8, *an*).
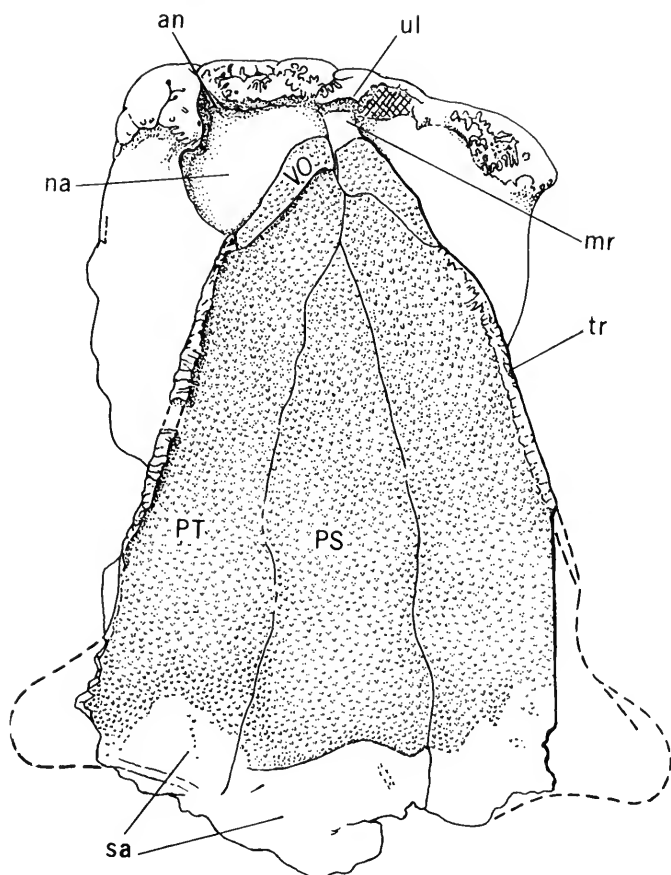
Fig. 8.   Palate and upper lip of *Uranolophus wyomingensis*, n. sp., PF 3805
(× 1).   *an*, anterior naris; *mr*, median ridge; *na*, position of nasal capsule; *PS*,
parasphenoid; *PT*, pterygoid; *sa*, smooth, untuberculated areas of pterygoids and
parasphenoid; *tr*, tooth ridge; *ul*, upper lip; *VO*, vomer.

The lateral border of each anterior naris is formed by a lateral proc-
ess, which is a continuation of the "upper lip" (="subnasal ridge"
of Jarvik, 1964, p. 44, figs. 12–14).   This lies at the lateral corner of
the downturned snout in *Uranolophus*, but is usually some distance
antero-medial to this corner in *Dipterus*.   The oral edge of the upper
lip in *Uranolophus wyomingensis* (fig. 7B), including both median and
lateral processes, usually has the dentine developed in sharp ridges,
irregular projections, and tubercles, similar to those on the lateral
edges of the pterygoids.   Since this is the only type of "teeth" de-
veloped in this species, it is of interest that they should occur in the

region corresponding to that occupied by the premaxillaries in other Osteichthyes. In *Dipnorhynchus sussmilchi* and most *Dipterus*, this border is probably smooth and toothless. However, "teeth" have been reported on the median process of one specimen of *Dipterus valenciennesi* (Watson and Day, 1916, p. 33), in *D. oervigi* (Gross, 1964, pp. 11–14), and in *Ganorhynchus woodwardi* (Traquair, 1873, p. 553). Possible vestiges of toothed premaxillaries or maxillaries have been described in *Scaumenacia* (Stensiö, 1947, p. 140, fig. 32B) and *Phaneropleuron* (Watson and Day, 1916, p. 36, fig. 7), in both of which the snout is otherwise largely unossified. A slender, toothless maxilla has been identified in *Dipterus* by Watson and Gill (1923, p. 206, fig. 32).

On the ventral surface of the neurocranium, immediately behind the upper lip and in front of the palate, there is a median ridge, on either side of which is a depression forming part of the nasal capsule. The structure of this region is best known among fossil lungfishes in *Chirodipterus* (Säve–Söderbergh, 1952, fig. 3) and *Ganorhynchus* (Gross, 1965, fig. 1); it has been figured in *Dipterus* (Jarvik, 1954, fig. 36B), and can be seen in two specimens of *Uranolophus wyomingensis* (PF 3792, fig. 10B; 3805, fig. 8), though the latter are so flattened that most details are obscured. The most obvious difference in *Uranolophus* is that this region is relatively short. This fact, together with the corresponding shortness of the prepineal part of the skull roof, are doubtless related to a comparatively poor development of the nasal organs in *Uranolophus*. The median ridge (fig. 8, *mr*) is broad in *Uranolophus*, as in *Dipterus*, but is shown by Gross to be very narrow in *Ganorhynchus splendens*. In the latter, the roof of each nasal pit has a recessus anterior leading into the anterior naris, and a recessus posterior, which was thought by Gross (1965, p. 117) to correspond in position to the posterior naris. This would place the posterior naris approximately in the same position as in *Neoceratodus* (Günther, 1872, pl. 34, fig. 3); however, Traquair (1878, pl. 3, fig. 1), Goodrich (1909, fig. 210A), Jarvik (1954, fig. 36B), and Thomson (1965, p. 222) have given it a more antero-lateral position, just postero-lateral to the process of the upper lip that forms the lateral margin of the anterior naris.[1] A well-preserved specimen of *Dipterus valenciennesi* in Field Museum collections (PF 1293) shows the anterior and posterior recessi in the same positions as in *Ganorhynchus*, with the posterior one far removed from the position of the

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[1] Jarvik, 1964, p. 44, has changed his opinion and places the posterior naris as in recent Dipnoi.

posterior naris indicated by Traquair, Goodrich, and Thomson. If the recessus posterior did actually house the posterior part of the nasal organ, it is likely that Gross is correct in assuming a position for the posterior naris well back near the palate and far removed from the margin of the mouth. Because of flattening, the recessi are not visible in specimens of *Uranolophus*, but in all *Uranolophus* and *Dipnorhynchus* the processes that bound the anterior nares laterally lie at the lateral corners of the upper lip, and there are no notches lateral to them.

The palate of *Uranolophus wyomingensis* (figs. 8, 9, 10B) is distinctive in three respects. First, it is relatively long, reaching from a point close to the median process of the upper lip at least as far back as the quadrate, which has a position considerably farther posterior than in *Dipterus*. Secondly, there are no palatal tooth plates; the whole ventral surface of the palate is covered with denticles, and on the lateral margins of the pterygoids the dentine has developed into an irregular "tooth ridge" or, occasionally, into isolated teeth. The palate is also distinctive in that the parasphenoid lacks a posterior stem.

The elements of the entire palates of *U. wyomingensis* are usually so closely fused that it is impossible to determine the extent of individual bones. However, in PF 3805 (fig. 8) and 3796 (fig. 9B), the former showing the ventral and the latter the dorsal surface of the palatal bones, the sutures can be determined satisfactorily. These specimens show that the pterygoids (fig. 8, *pt*), or more properly the entopterygoids, are very long and relatively narrow, and taper slightly and irregularly anteriorly. They are broadest posteriorly where they expand laterally underneath the quadrates. The posterior part of the lateral margin of each pterygoid, which underlies the quadrate, is smooth and concave, but much of the rest of the margin carries a "tooth ridge" (fig. 8, *tr*), which will be described further below. Anteriorly the pterygoids meet or overlie the vomers, and in the midline behind the vomers the two pterygoids meet in a relatively short suture. Most of the medial edge of each pterygoid is a suture with the long parasphenoid. The posterior edges of the pterygoids curve dorsally and share a smooth, untuberculated area (fig. 8, *sa*) with the parasphenoid.

The paired vomers are the smallest of the palatal bones. In PF 3805 (fig. 8, *vo*) they meet in a short median suture, then curve backward around the anterior ends of the pterygoids, becoming narrower posteriorly. Their ventral surfaces are tuberculated, but their
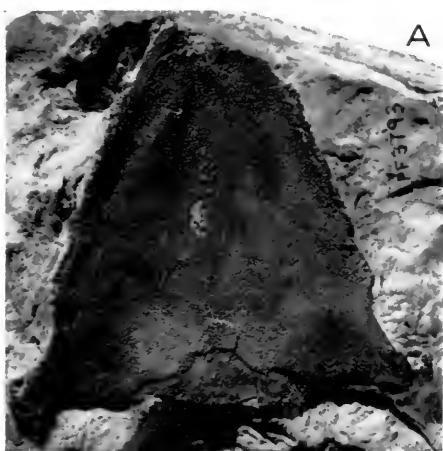
FIG. 9. Palates of *Uranolophus wyomingensis*, n. sp. (× 2/3). A, PF 3793, ventral surface; B, PF 3796, dorsal surface.

lateral margins lack "tooth ridges." The nature of their suture with the pterygoids is not clear, but it looks in PF 3805 as if the pterygoids were underlain by the vomers. This is the relationship shown by Gross (1964, p. 18, fig. 2B) in *Dipterus oervigi* between a pterygoid and a bone identified as a palatine or vomer. The vomers of *Dipnorhynchus sussmilchi* (Campbell, 1965, pl. 91) are similar in general, forming a blunt, arrow-shaped point at the anterior end of the palate. In *D. lehmanni* there is what is described by Westoll (Lehmann and Westoll, 1952, p. 410) as "a flanged surface, probably for the overlapping vomers"; this surface resembles in shape the vomers of *U. wyomingensis*. In *Dipterus* and most other lungfishes, the vomers are much reduced, perhaps because of the predominant development of the pterygoid tooth plates. White (1965, pp. 39–41) found no confirmation of the presence of relatively large vomers such as were shown in a restoration of *Dipterus valenciennesi* by Watson and Day (1916, p. 33, fig. 6). It is interesting that in *Fleurentia*, where tooth plates are lacking, the vomers were probably relatively large, as in *Dipnorhynchus* and *Uranolophus*.

The parasphenoid of *Uranolophus wyomingensis* (fig. 8, *PS*) is a long, slender bone, occupying about one-third of the width of the palate posteriorly, and tapering with some sutural undulations to a point near the anterior end of the palate. In only two other lungfishes is it known to extend as far forward: one of these is *Dipnorhynchus lehmanni*, where Westoll (Lehmann and Westoll, 1952, fig. 4B) shows it as a very narrow plate, though its outline is not known with any certainty; and the other is *Uronemus*, where it is shown by Watson and Gill (1923, fig. 29B) to be very broad. The ventral surface of the parasphenoid of *U. wyomingensis* is denticulate, except at the posterior end where there is a wide, smooth area (fig. 8, *sa*), shared with the pterygoids, presumably for the overlap of more posterior plates. Since the parasphenoid of *Uranolophus* completely lacks the long, posterior stem that is characteristic of other Dipnoi, it is possible that this area was overlapped by separate parotic plates. Westoll (Lehmann and Westoll, 1952, p. 415) has already suggested that separate parotic plates may have been present in *Dipnorhynchus*, just as they are in crossopterygians (Jarvik, 1954, figs. 22, 25). Parotic plates possibly occur in place in one specimen of *Uranolophus wyomingensis*, PF 3792 (fig. 10B), but, unfortunately, this specimen has lost the posterior end of the parasphenoid and the anterior ends of the possible parotic plates, though they have been preserved in part as a plastic cast of their natural mold. What is actually left is
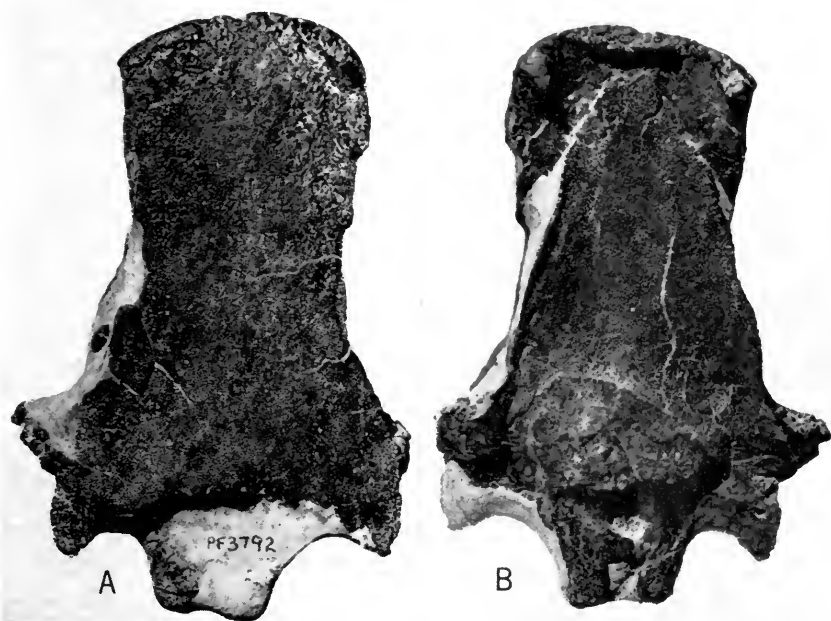
Fig. 10. Nearly complete skull of *Uranolophus wyomingensis*, PF 3792 (× 3/4). A, dorsal view; B, ventral view.

a broken bone, or more probably a pair of bones, lying at the midline behind the parasphenoid, and projecting posteriorly well behind the posterior border of the cranial roof.

The dorsal or cranial surface of the palate is well shown in PF 3796 (fig. 9B). The parasphenoid is largely spongy bone on this surface and was probably closely applied to the ventral surface of the neurocranium. Centrally, it has an area covered with compact bone, and in the posterior part of this area is a depression which was probably occupied by the hypophysis. *U. wyomingensis* has no hypophysial canal penetrating to the ventral surface of the parasphenoid, such as may occur in *Dipnorhynchus*, *Dipterus*, and *Rhinodipterus* (White, 1965, p. 39). The vomers cannot be distinguished as separate elements in PF 3796, perhaps only because the sutures are obscure, or perhaps because they are overlain by the pterygoids. The pterygoids of PF 3796 and isolated specimens (PF 3807, 3867) are well defined and largely covered on their dorsal surface by compact bone. Overlying the "tooth ridge" is a sharp ridge (fig. 4, *pr*) which rises above the anterior and posterior ends of the "tooth ridge" into prom-

inent processes whose medio-dorsal surfaces lack the compact bone. These processes are the points of attachment of the pterygoid, but the nature of this attachment is difficult to ascertain. Similar processes may occur in *Dipnorhynchus sussmilchi* (White, 1965, p. 36), but Säve–Söderbergh (1952, figs. 2, 5) shows nothing comparable in *Chirodipterus*, where the pterygoids apparently are closely applied to the ventral surfaces of the palato-quadrate and neurocranium. In *Dipterus* White (1965, p. 35, fig. 45) has described two "buttresses" on the lateral wall of the endocranium, an anterior one formed by the lateral part of the planum antorbitale, and a posterior one in the anterior part of the orbito-temporal region. These buttresses overlie the tooth plates, just as the dorsal processes of the pterygoids overlie the ends of the tooth ridges of *Uranolophus wyomingensis*. They are assumed to be endocranial ossifications, but it is not possible to determine their boundary with the dermal bones. In *Neoceratodus*, where the endocranium is completely cartilaginous, each pterygoid tooth plate is braced by processes of dermal bones. One is a process descending from the largest paired cranial roofing bone; this splits into two processes which extend to the pterygoid, one near the anterior part of the tooth plate, and the other near its posterior part. The pterygoid has an ascending process which rises just anterior to the middle of the tooth plate and inter-fingers with the descending process. These processes appear to be parts of the dermal bones to which they are attached, and they lie against the lateral wall of the neurocranium just anterior to the orbital region. The relationships of the processes that brace the tooth plates of *Neoceratodus* are very similar to the "buttresses" of *Dipterus*, except that they are formed by dermal bones in the former, and probably by endocranial bones in the latter. It is possible that as ossification of the cranium was reduced during lungfish evolution, the dermal pterygoids and cranial roofing bones enlarged their processes to take over the bracing function that was earlier performed largely by endocranial ossifications.

Cheek, opercular and gular plates.—In addition to several isolated opercular, gular, and probable cheek plates of *Uranolophus wyomingensis*, the partially articulated type specimen (PF 3874, fig. 2) shows some of them, but, unfortunately, scattered from their natural positions so that it is not possible to determine their precise arrangement. This is particularly true of the circumorbital and cheek plates, but while this region cannot be reconstructed, it is possible to demonstrate that the cheek was relatively much longer in *Uranolophus* and *Dipnorhynchus* than in other lungfishes, as already indicated by Hills (1933, p. 641) and Westoll (1949, p. 142, fig. 5A). This is shown by
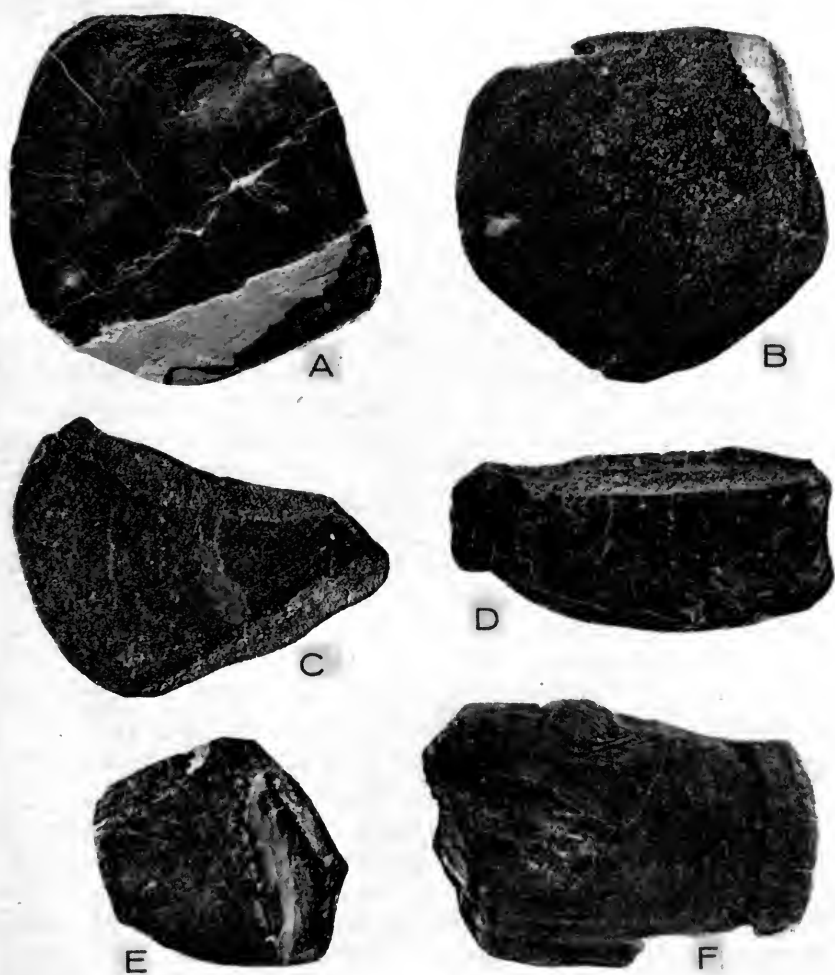
FIG. 11. Operculars and gulars of *Uranolophus wyomingensis* ($\times$ 2/3). A, inner face of opercular, PF 3835; B, outer face of opercular, PF 3839; C, second subopercular, PF 3836; D, first subopercular, PF 3862; E, antero-lateral gular, PF 3866; F, principal gular, PF 3838.

the position of the fused quadrate, which extends ventrally and a little anteriorly from the level of the posterior part of Y_1. The opercular must have attached immediately behind this suspensorium, and the relatively wide space between it and the orbit was occupied in life probably by a number of relatively large cheek and circumorbital plates. *Soederberghia* and *Rhynchodipterus* retain a moderately long cheek with relatively large plates, but in other adequately known Dipnoi the cheek is much shortened, and the plates small and reduced in number. This has resulted from the forward shift of the jaw articulation and from the more posterior position of the orbits.

The opercular (figs. 11 A–B) is the biggest plate on the skull, attaining a length of 100 mm. and a height of 73 mm. in the largest individual in the collection (PF 3862). Its shape is variable, and changes with age, as is indicated by growth lines, which are sometimes prominent on the inner surface (fig. 11A). The center of growth is near the antero-dorsal corner, which in life must have occupied a position at the edge of the skull roof near the boundary of Y_1 and Y_2. The dorsal edge lay against Y_2, and also against scales or bone Z, behind Y_2. The anterior edge is usually quite straight, and presumably attached at or close behind the quadrate. The posterior and ventral edges are rounded, and in PF 3870 there is a deep notch in the ventral edge which, as is indicated by growth lines, appeared quite late in development. The attachment of the operculum is quite similar to that of *Dipterus*, where often there is a laterally projecting angle on Y_1 that lay against the antero-dorsal corner of the opercular.

Two subopercular may be present in *Dipterus* (Graham–Smith and Westoll, 1937, fig. 2a) and *Scaumenacia* (Stensiö, 1947, fig. 32B), and it is thought that this is true in *Uranolophus wyomingensis*, also. If these bones are correctly identified and oriented (fig. 12), the subopercular are relatively much larger in *Uranolophus*, even larger than restored by Westoll (1949, fig. 5A) in *Dipnorhynchus*. Subopercular 1 (fig. 11D) is a bone with rather uniform width; dorsally it has a relatively wide area overlapped by the operculum, and anteriorly a small area overlapped by a cheek plate or postmandibular bone. Subopercular 2 (fig. 11C) is narrow anteriorly and wide posteriorly; dorsally it has a wide area overlapped by subopercular 1, ventrally a wide area overlapped by the principal gular, and anteriorly a very small overlap area for postmandibular bone (fig. 12, *oa*). A single subopercular is retained in some other fossil lungfishes and in *Neoceratodus*, but it is never as largely developed as the subopercular of *Uranolophus*.
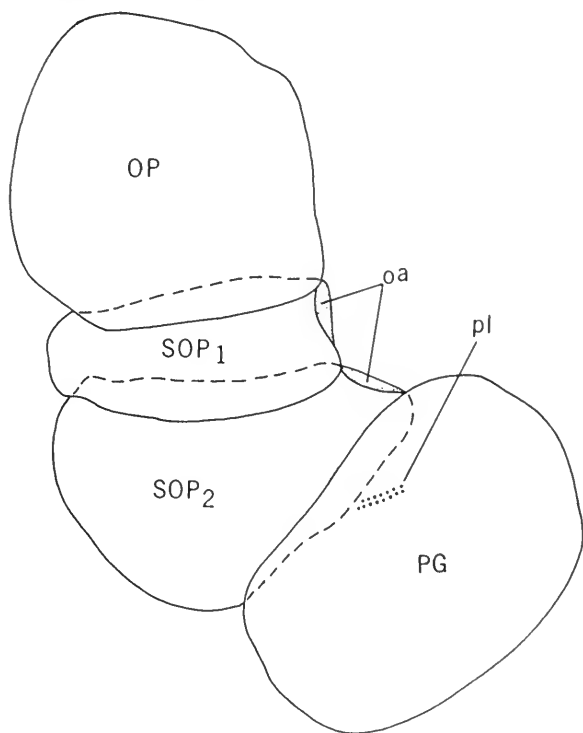
Fɪɢ. 12.   Attempted restoration of right operculars and principal gular of *Uranolophus wyomingensis*, n.sp.   *OP*, opercular, based on PF 3835; *PG*, principal, gular, restored from PF 3838; *SOP*₁, first subopercular, based on PF 3862; *SOP*₂, second subopercular, based on PF 3836 (*SOP*, about × 1/2; others slightly larger); *oa*, overlap areas for cheek plates or postmandibular bones; *pl*, pit line.

Gular plates are preserved in the partially disarticulated head of the type of *Uranolophus wyomingensis* (PF 3874), but they are buried under the lower jaws, ceratohyal, and other elements, so their number and shape are not determinable.   A few large, isolated plates can be tentatively identified as gulars on the evidence of the conditions in *Dipterus*, as figured by Watson and Gill (1923, fig. 33) and Graham–Smith and Westoll (1937, fig. 2a).   The smaller ones (PF 3866, fig. 11E; 5519) are believed to be paired antero-lateral gulars; they have an anterior area that may have been overlapped by an antero-median gular, and a median area that may have been overlapped by the antero-lateral gular of the opposite side.   Their antero-lateral edges presumably lay against the lower jaws unless there were sub-mandibular elements in between, such as Jarvik (1963, p. 13) has identified in crossopterygians.   Their posterior edges probably overlapped

the principal gular and a median gular. One plate (PF 3838, fig. 11F) has been tentatively identified as postero-lateral or principal gular. It is one of the largest known plates of *U. wyomingensis*, with a preserved length of 82 mm. It differs from opercular plates in that its center of growth, as shown by growth lines, is near the center of its presumed anterior end, and also in its relatively longer form. Near one side of the exposed inner surface there are some short ridges which possibly indicate the pit lines that occur on the principal gulars of other Dipnoi. As placed in the restoration (fig. 12), this gular overlaps the ventral edge of subopercular 2; however, neither the lateral nor medial edge is completely preserved

Lower jaws.—The lower jaws of *Uranolophus wyomingensis* are similar in general features to those of *Dipterus* except that they lack ridged tooth plates and are relatively longer. The length of the lower jaws (measured from the midline anteriorly to the articular) is about 78 per cent of the median length of the cranial roof (excluding extrascapulars) in the articulated type specimen of *U. wyomingensis* (PF 3874). In *Dipterus valenciennesi* the same ratio, estimated from PF 1293, is about 67 per cent. The relatively greater length of the jaws of *Uranolophus* is related to the more posterior position of their articulation.

The names that have been used for the dermal bones of the lower jaw have been based on assumed homologies with the jaw bones of other fishes, particularly rhipidistians. In view of the situation of the cranial roof, where strict homologies with rhipidistian bones are clearly impossible in most cases, it may be questioned whether it serves any useful purpose to attempt homologies of the lower jaw elements. All of the lower jaws from Cottonwood Canyon are cosmine covered ventrally and laterally, and so usually no sutures are visible. However, on the ventral surface of the symphysial region one large specimen (PF 3797, fig. 13A) shows grooves in the cosmine which resemble incomplete sutures; these divide this area partially into what appears to be a mosaic of small plates. This recalls the snout of PF 3805, which is similarly divided, and suggests that the ancestral dipnoan may have had a lower jaw covered with a mosaic of small dermal bones. If so, they may have enlarged or fused during evolution in a manner different from that in rhipidistians, making strict homologies impossible. Since non-committal names are not available, the names used by Watson and Gill (1923) will be employed, but with reservations.
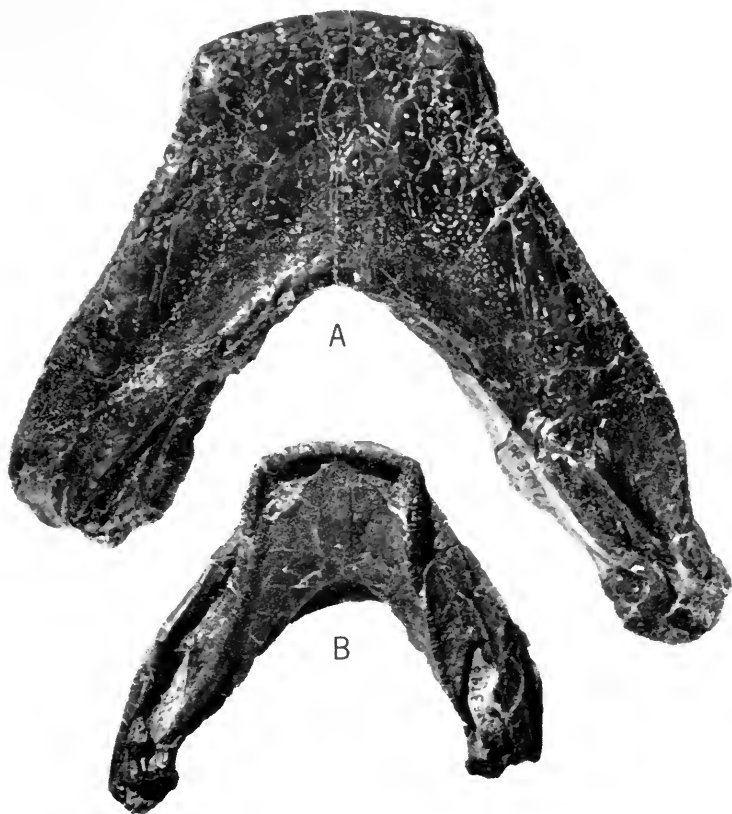
FIG. 13.   Lower jaws of *Uranolophus wyomingensis*, n. sp. ($\times$ 3/4).   A, ventral view of PF 3797; B, dorsal view of PF 3798.

In a recent paper Jarvik (1967) has introduced new notations for the dermal bones of the dipnoan lower jaw.   These are meritorious in as far as the notations imply no homologies with the bones of other fishes, but as Jarvik used them within the lungfishes, they indicate his assumption of bone fusions, for which evidence is largely lacking. The notations are based in large part on his new Devonian genus, *Melanognathus*, where four distinct sensory canal bones are preserved on each side, and the presence of a fifth one is assumed.   Since this arrangement is unique among lungfishes, it is hardly proper to assume that it is primitive, as did Jarvik, or to use it as a basis for comparison of other genera.

Around the anterior end of the jaw, the dentaries form an erect, nearly rectangular margin, which is entirely surmounted by a "tooth ridge" (fig. 13B). Instead of being shaped like a smoothly-rounded semi-circle, as in *Dipterus* and *Holodipterus*, they have a nearly straight, transverse, anterior edge, which is separated by sharp curves from the nearly straight, antero-posteriorly directed, lateral rims. The dentaries are well separated from the prearticulars, except posteriorly where they meet them in well-marked sutures (fig. 14A). In PF 3797 (but not in PF 3798) the dentaries have small, triangular, denticulated surfaces between these sutures and the tooth ridges. Anteriorly, the dentaries are cosmine covered and pass without visible sutures into the ventral bones of the symphysial region. Laterally, each dentary overlies on the side of the jaw an elongate fossa (fig. 14A, *fo*) which was probably occupied in life by a fold of the lower lip (Jarvik, 1964, p. 44).

On the ventral and lateral surfaces of the jaw of specimens from Cottonwood Canyon (fig. 13A) individual bones usually cannot be distinguished because of the cosmine coating. One incomplete lower jaw from Beartooth Butte (PF 3318) has lost much of its bone, but does show probable sutures dividing the lower and lateral surfaces into three pairs of bones very similar to the splenials, postsplenials, and angulars figured in *Dipterus* by Watson and Gill (1923, fig. 34). The specimen of ?*Dipnorhynchus* from Australia figured by Hills (1935, fig. 1) shows on one side the radiation of three bones that are also closely comparable. The splenial and postsplenial (fig. 14B, *SP*, *PSP*) lie below the symphysis and postero-lateral to it. The angular (fig. 14B, *AN*) is the most posterior of these bones and extends nearly to the posterior tip of the jaw, where it lies on the lateral side of the articular; in front of the articulatory area it forms the lateral margin of the adductor fossa.

The prearticulars (fig. 14A, *PR*) cover most of the medio-dorsal surfaces of the lower jaws. Most anteriorly they do not meet the dentaries, as in *Dipterus* and *Holodipterus*, but form a blunt point separated from the dentaries by a short distance. Laterally, they suture with the posterior ends of the dentaries, but in front of each suture is a sub-triangular space that is floored by what is probably an ossification of Meckel's cartilage (fig. 14A, *MK*). The prearticulars show no suture where they meet in the midline. Their posterior margin near the midline in the symphysial region is separated from the underlying splenials by a gap that was probably occupied by Meckel's cartilage and has been reduced by crushing in Cottonwood Canyon
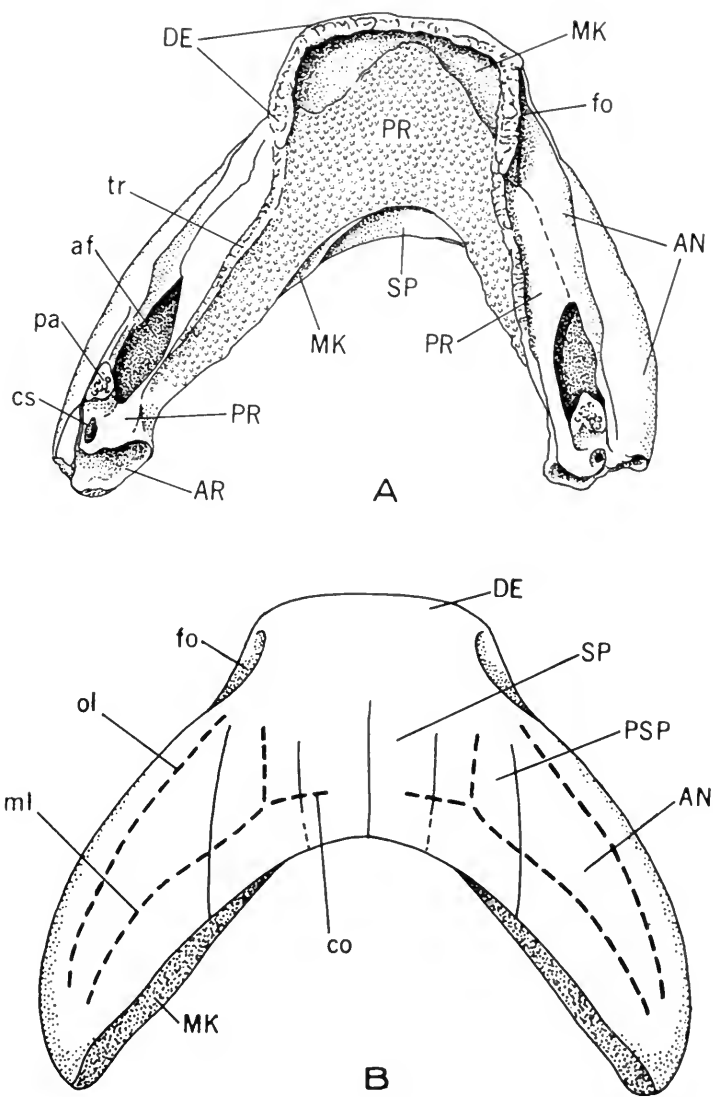
FIG. 14. Lower jaws of *Uranolophus wyomingensis*, n. sp. (× 1). A, dorsal view of PF 3798; B, ventral view, restored largely from PF 3318 and 3798. *af*, adductor fossa; *AN*, angular; *AR*, articular; *co*, commissure between mandibular sensory canals; *cs*, undetermined foramen; *DE*, dentary; *fo*, fossa for fold of lower lip; *MK*, ossification of Meckel's cartilage; *ml*, mandibular sensory canal; *ol*, oral sensory canal; *pa*, processus angularis; *PR*, prearticular; *PSP*, postsplenial; *SP*, splenial; *tr*, tooth ridge.

material.   Here were attached the retractor muscles of the lower jaws, while the anterior gular lay below them in a superficial position.

Each prearticular is surmounted by a "tooth ridge" (fig. 14A, *tr*) which continues that of the dentary, and extends posteriorly about to the middle of the adductor fossa.   In this area of the lower jaw of *Holodipterus*, Gorizdro–Kulczycka (1950, p. 88) described three pairs of conical teeth on what she identified as coronoids.   Since no sutures are shown in her drawings nor described in the text, it is doubtful whether there were separate coronoid ossifications in this or any dipnoan.   Medial to the tooth ridge, the prearticular is denticulate, except on its medio-ventral edge.   This medial lamina extends nearly to the medio-ventral edges of the angular and postsplenial, but is separated from them by a space filled by a presumed ossification of Meckel's cartilage (fig. 14A, *MK*).   Posteriorly, the medial lamina extends nearly to the posterior end of the jaw, where it surrounds the articular on its medial and ventral sides.   Laterally to the "tooth ridge" the prearticular has a smooth, non-denticulate lamina that becomes very narrow posteriorly where it bounds the medial side of the adductor fossa (fig. 14A, *af*).   The lateral lamina reaches as far back as the articulation, just anterior to which it rises up to form much of the processus angularis (fig. 14A, *pa*).   The latter has globular ossifications on its crown which may represent ossifications of an ascending or coronoid process of Meckel's cartilage.   Just behind the processus angularis the prearticular is pierced by a large foramen (fig. 14A, *cs*) comparable to the foramen "c.s." described by Gross (1956, pp. 28, 32) in other lungfish and crossopterygians.

The articular ossification (fig. 14A, *AR*) appears in the glenoid fossa for the quadrate, which is a deep groove, not quite transverse, but oriented a bit anterior of medially.   Its ventral surface is nearly horizontal, while its anterior surface is strongly concave and vertical.   The whole surface of the articular is covered with irregular, globular ossifications.

Teeth.—The pterygoids and prearticulars of *Uranolophus wyomingensis* completely lack the ridged tooth plates that characterize the majority of lungfishes.   Instead, they have evolved what has been described above as "tooth ridges."   On the palate each "tooth ridge" (fig. 8, *tr*) appears on the lateral edge of the pterygoid just in front of the sharp curvature where that bone expands laterally under the quadrate; it extends forward along the lateral edge of the pterygoid to the suture with the vomer, but not onto the vomer.   On the lower jaw the "tooth ridge" (fig. 14A, *tr*) rises on the dorsal edge of

each prearticular opposite the middle of the adductor fossa; it extends anteriorly nearly continuously along the prearticular, onto the dorsal edge of the dentary, and around the front of the jaw into the prearticular "tooth ridge" of the opposite side. The continuity of this ridge is interrupted slightly at the prearticular-dentary suture, where the prearticular ridge continues mediad to the dentary ridge along the margin of the prearticular.

The ridge itself forms a continuous crest, sometimes irregular, and typically modified by the development on its inner and outer sides of numerous vertical ridges at right angles to the main ridge (fig. 15). Both the main ridge and the side ridges are composed of dentine. The side ridges are often more strongly developed on the lateral side, while on the medial side and at the posterior end of the "tooth ridges" they grade into elongate and then conical denticles. In some specimens the side ridges are weakly developed and take the form of elongate denticles. Other specimens (PF 3807, 3867) show lateral to the "tooth ridge" a row of isolated, conical teeth, resembling those of *Griphognathus minutidens* (Gross, 1956, fig. 27). These may be considered as side ridges that have developed independently from the main "tooth ridge," since they are comparable in shape to some of the adjacent side ridges. One specimen (PF 3816) completely lacks "tooth ridges" on the pterygoids; where they usually occur are rounded edges composed apparently of bone only partially covered by dentine.

The crests of the main and side ridges are usually blunted, presumably by wear. Such worn ridges usually have a flat crest separated by sharp edges from the sides. In some specimens the amount of wear is slight, the ridges remain prominent, and low side ridges, or the bases of larger side ridges, may remain sharp and unworn. In one specimen (PF 3792, fig. 15D) the main ridge has worn low and the side ridges are much reduced.

The anterior, transverse part of the dentary, and of the upper lip which over-rides it (fig. 7B), are developed differently from the rest of the "tooth ridges." On the posterior faces of the dentary and upper lip there may be side ridges, but usually they are not as prominent as more posteriorly. Anterior to these posterior faces the dentine shows great variability in its development. It may be relatively continuous, but hollowed out into irregular, shallow depressions; or it may be pierced by deep grooves and pores which divide it into a pattern of irregular areas, simple or branched ridges, projections, or denticles.

The bones of the palate (pterygoids, vomers, and parasphenoid) and the medial laminae of the prearticulars are covered with small, conical denticles, composed of dentine. These denticles are commonly larger anteriorly, and also near to the "tooth ridges," where they may be developed as short, sometimes branching ridges. The palate and prearticular may show an occasional patch of larger denticles, and one palate (PF 3793, fig. 9A) is notable for an oval, elevated area near the center of the parasphenoid covered with sinuous, branching ridges and elongate denticles composed of dentine.

There are a number of genera of lungfishes in which ridged dental plates are lacking, but none has evolved anything exactly comparable to the "tooth ridges" of *Uranolophus wyomingensis*. The "teeth" of *Dipnorhynchus lehmanni* (Lehmann, 1956, pl. 1, fig. 2) and *Ganorhynchus splendens* (Gross, 1965, fig. 1B) are knob-like prominences arranged along the lateral edges of the pterygoids in two rows; some of the prominences are confluent at their bases in *G. splendens* and perhaps in *D. lehmanni*, though the only specimen of the latter is too poorly preserved to be sure. *Uronemus splendens* has one or two rows of "large, compressed, conical teeth" on the margins of the pterygoids and on the prearticulars (Watson and Gill, 1923, p. 204, fig. 30; Graham-Smith and Westoll, 1937, p. 261); the teeth appear in the figure to be confluent at their bases and thus to form a sort of "tooth ridge." *Griphognathus minutidens* (Gross, 1956, p. 36, fig. 27) has one or more rows of small, conical teeth on the prearticular, but usually they remain distinct and do not unite at their bases. *Holodipterus sanctacrucensis* (Gorizdro-Kulczycka, 1950, pp. 89–90, fig. 2:1) has three pairs of large, isolated, conical teeth, presumably on each prearticular. *Fleurantia denticulata* (Graham-Smith and Westoll, 1937, p. 249, fig. 9) has conical teeth arranged in radial rows on the palate, but not forming a distinct tooth plate. Perhaps the most aberrant development is in *Dipnorhynchus sussmilchi*, which has three large, bulbous masses on the palate (Campbell, 1965, p. 635) and similar structures on the lower jaws (White, 1966, p. 7, pl. 1, fig. 1); as White has shown, they are composed of dentine underlain by spongy bone. At least two genera, *Soederberghia* and *Conchopoma*, lack teeth entirely, but have the palate and prearticular covered with denticles.

Fig. 15. Tooth ridges of *Uranolophus wyomingensis*, n. sp. ($\times$ 8). A–B, left pterygoid of PF 3805, A, anterior part and B, middle of ridge; C–D, right pterygoid of PF 3792, C, middle and D anterior part of ridge; E, probable prearticular ridge, PF 3864.

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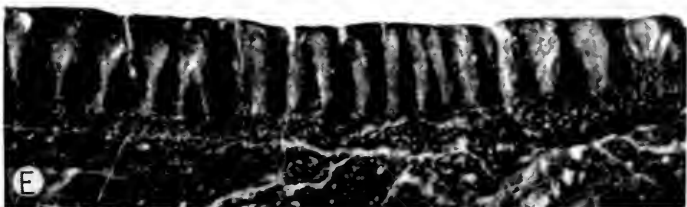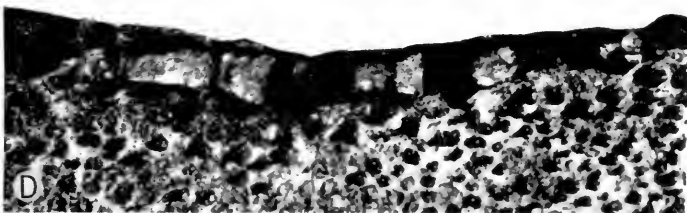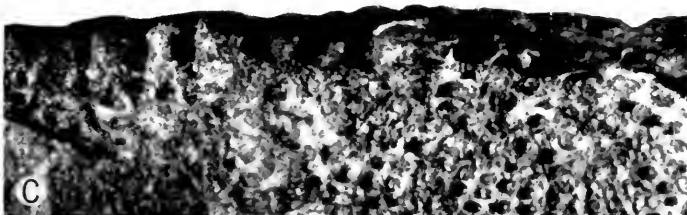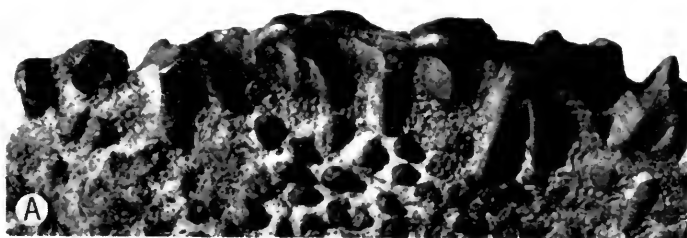
Watson and Gill (1923, p. 214) believed that *Uronemus* and *Conchopoma* were derived from ancestors with typical tooth plates. They argued that the whole structure of the dipnoan skull was specially modified for the use of crushing tooth plates, and that the skull and tooth plates must have evolved together. According to them, the presence of isolated teeth in *Uronemus* was a neotenic character, and this is possible because in the modern *Neoceratodus*, as shown by Semon (1901, pp. 116–122), the teeth arise as isolated denticles and only later fuse to a bony base to form a tooth plate. Lehman (1959, p. 34) also concluded that the presence of denticles instead of tooth plates on the palate of *Soederberghia* was a neotenic character. To me it seems more probable the dipnoans without tooth plates evolved from an ancestor which had not yet evolved these specialized structures. As the marginal jaw bones were reduced and lost in early dipnoan history, the palate and prearticulars evolved a variety of biting structures, of which the typical dental plate with radiating ridges was only one. Some lungfishes, such as *Soederberghia* and *Conchopoma*, simply retained the primitive denticulation. Others such as *Griphognathus*, *Ganorhynchus*, *Uronemus*, *Holodipterus*, and *Dipnorhynchus lehmanni*, enlarged denticles on the margins of the palate and on the prearticulars to form one or more rows of teeth. In *Uranolophus* such individual tooth elements were fused to form a ridge. *Dipnorhynchus sussmilchi* is quite isolated in developing whole areas of the palate and lower jaws as bulbous, crushing surfaces. This view of dipnoan dental evolution has an important bearing on classification, since those genera without tooth plates would not be derived from, nor closely related to, those genera that did possess such structures.

Endocranium and visceral skeleton.—All of the skulls of *Uranolophus wyomingensis* in the collection have been greatly flattened and, as a result, their endocrania have been crushed to such an extent that they show little or none of their structure. One moderately large skull (PF 3816) was partially prepared on the ventral surface in order to examine the posterior part of the endocranium. This proved to be so extensively crushed that it was of little use; it did show, however, that there were both perichondral ossifications as well as spongy endochondral bone. In this respect, *U. wyomingensis* agrees with *Dipterus* and *Chirodipterus*, and differs from later lungfishes in which the ossification of the endocranium was reduced or lost.

The partially articulated type specimen of *Uranolophus wyomingensis* (PF 3874, fig. 2) preserves a number of elements of the hyoid

and branchial arches (and possibly cranial ribs), but they are displaced enough so that identification of individual elements, with one exception, is probably not possible. The largest is surely a ceratohyal, an element also known isolated in three other specimens (fig. 16).

FIG. 16.   Ceratohyal of *Uranolophus wyomingensis*, n. sp., PF 5514 ($\times$ 1).

It is a long bone, laterally compressed as preserved, tapering at both ends, and curved so that its ventral edge is convex and its dorsal edge is nearly straight. At its proximal end is an unossified area, facing postero-dorsally, presumably cartilaginous in life. There appears also to be a smaller unossified area at the distal end for attachment to a hypohyal. In other fossil lungfishes whose ceratohyals have been described (*Fleurantia, Soederberghia, Jarvikia, Uronemus, Conchopoma*) and in the modern *Neoceratodus*, the ceratohyals have a different and characteristic shape; they are rod-shaped bones distally and expand to deep, laterally compressed blades proximally. In *Lepidosiren* the ceratohyal is similar except that the proximal end, while laterally compressed, is not much expanded. What I identify as ceratohyals in *Dipterus* (PF 1294, UC 2217) are well-ossified, robust rods, tapering slightly distally, and laterally compressed proximally. In all lungfishes the ceratohyal probably had a cartilaginous core and the ossification is superficial.

Almost certainly a number of the rod-like bones behind the skull of the partially articulated *U. wyomingensis* (PF 3874, fig. 2) are branchial arch elements. Although these cannot be individually identified, they are of interest because this is the only lungfish, with the possible exception of *Conchopoma* (Weitzel, 1926, p. 168), in which branchial arches are known to be ossified. This is additional

support for the widely accepted view that primitive Dipnoi had a well-ossified skeleton.

Lateral-line system.—None of the material of *Uranolophus wyomingensis* from Cottonwood Canyon has been prepared to show the canals of the lateral-line system, so their course can only be inferred from the distribution of the pores by which the tubuli open on the surface. As indicated by White (1965, p. 9), this can lead to erroneous interpretations. However, a skull (PF 1427, fig. 3A) and lower jaws (PF 3318, fig. 14B) from Beartooth Butte, show the actual course of some of the canals, which are preserved as sedimentary fillings, or as impressions of fillings on the surface of dermal bones. On the cranial roof, the arrangement of the canals agrees closely with that of *Dipnorhynchus sussmilchi*, as figured by Hills (1941, figs. 1, 5). The supraorbital canals start in the posterior part of J, extend anterolaterally to L_1 and L_2, where they curve antero-medially onto M; more anteriorly they are not indicated on PF 1427. A specimen from Cottonwood Canyon (PF 3805) has on the anterior part of the skull roof a pore distribution which can be interpreted to indicate supraorbital canals with similar courses to those of *Dipterus valenciennesi* (fig. 3D), as shown by White (1965, fig. 18). The main lateral-line canal crosses Y_2, Y_1, and X, where it turns down into the infraorbital canal. At the point where it turns down, PF 1427 (fig. 3A) has on one side a branch extending antero-medially toward $L_1 + K$; though this cannot be traced to the supraorbital canal, it corresponds to part of the commissure connecting supra- and infra-orbital canals in *Dipterus*. The middle pit line is seen only as short grooves on I and Y_2 of PF 3874 (fig. 4, *pl*). No posterior pit line or occipital commissure has been identified, probably because it is developed as a canal within bone I; this is indicated by the presence of pores on this bone in PF 3816 and 3874 (fig. 4, *occ*), and of a short section of a filled canal on one bone I of the Beartooth Butte skull (PF 1427, fig. 3A). The same may apply to *Dipnorhynchus sussmilchi* (Campbell, 1965, p. 635). It is possible that the middle pit line is developed as a canal in PF 3816; no pit line is visible, but some pores do occur in the anterior part of I (fig. 5).

The sensory canals of the lower jaws are well shown on the Beartooth Butte specimen (PF 3318) as grooves on the impressions of the inner surfaces of the dermal bones. Each mandibular canal (fig. 14B, *ml*) runs parallel to the medio-ventral edges of the angular and postsplenial; in the latter bone it turns forward parallel to the postsplenial-splenial suture, and from the point of turning also sends a medi-

ally-directed commissure (fig. 14B, *co*) into the splenial. Presumably the commissure joins the mandibular canal of the opposite side, but its medial part is not preserved on this specimen. The oral canal (fig. 14B, *ol*) runs parallel to the dorso-lateral borders of the angular and postsplenial. The anterior parts of the lower jaws are not preserved, but it is probable from the courses of the canals that the oral and mandibular canals meet in the anterior part of the postsplenial. A similar canal pattern is indicated by pores on some of the lower jaws from Cottonwood Canyon and in *Dipterus* (Jarvik, 1964, fig. 14B).

Shoulder girdle.—The shoulder girdle of *Uranolophus wyomingensis* is known from four more or less complete cleithra, two attached but incomplete cleithra and clavicles, and one probable interclavicle. The partially articulated type specimen (PF 3874) is of little use since it shows only part of one cleithrum, overlain by an operculum.

The cleithrum (fig. 17A–C) consists of a rather narrow, elongate, dorsally-directed blade, and a shorter, antero-ventrally-directed ventral part. The dorsal blade lacks on its external surface (fig. 17C) any ridges such as occur in *Neoceratodus* and *Sagenodus*. Its anterior edge is concave, and its posterior edge is convex in its dorsal part and concave in its ventral part, terminating in a prominent angulation where it curves into the lower part. The outer face is cosmine-covered only along the posterior edge, and usually only on its dorsal part. More anteriorly the outer surface is covered with tubercles and ridges, probably indicating the area overlapped by the operculum. The inner surface of the cleithrum (fig. 18, *CLM*) shows a center of radiation nearly opposite the angulation between the dorsal and ventral parts. From this center a shallow depression extends to the antero-dorsal corner. The dorsal end of the cleithrum probably overlapped a plate, or the most ventral and posterior of a series of plates, that connected it to the skull. These plates have not been identified, nor is any overlap area clear. However, PF 3851 (fig. 17A) is unique in having a deep, V-shaped notch in the dorsal end of the cleithrum for the reception of such a plate.

The ventral part of the cleithrum has an external lamina that is continuous with the dorsal blade, and differs from it externally only in being directed more anteriorly. This lamina is ornamented on its outer face with tubercles and ridges, and is truncated anteriorly, except ventrally where it is prolonged into an anterior process; this process is strong in one specimen (fig. 17B), but is only weakly developed in another (fig. 17C). On the inner surface (fig. 18, *il*) is a clearly distinct, inner lamina, extending anteriorly from the center of
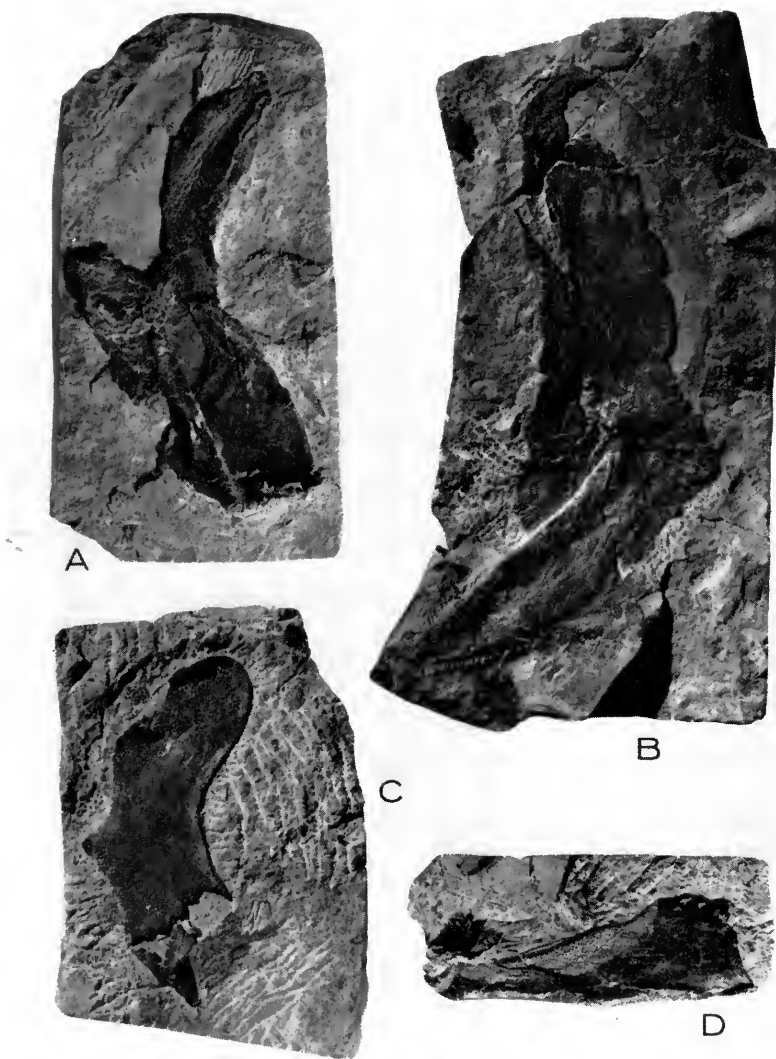
Fig. 17. Shoulder girdle elements of *Uranolophus wyomingensis*, n. sp. ($\times 2/3$). A, left cleithrum and incomplete clavicle, inner side, PF 3851; B, right cleithrum, inner side, PF 3846; C, right cleithrum, outer side, PF 3856; D, probable inter-clavicle, PF 3865.
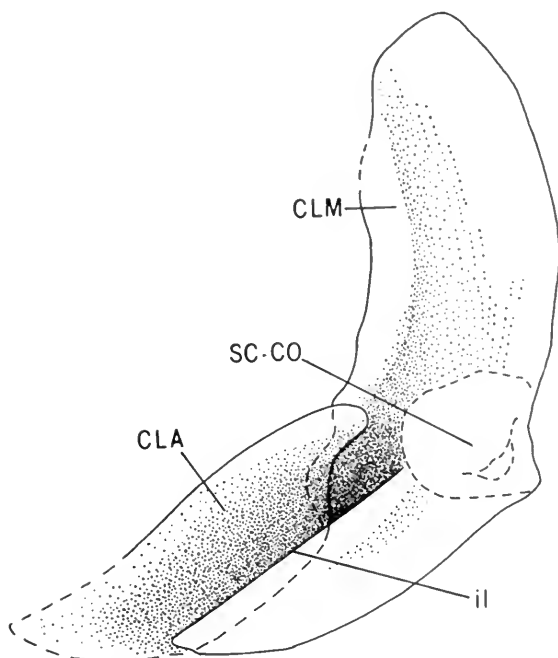
FIG. 18.   Inner side of right shoulder girdle of *Uranolophus wyomingensis*, n. sp., restored from PF 3846 and 3851. *CLA*, clavicle; *CLM*, cleithrum; *il*, inner lamina of ventral part of cleithrum; *SC–CO*, approximate position and extent of scapulo-coracoid.

growth of the cleithrum along its postero-ventral edge to the tip of the anterior process. The antero-dorsal edge of the inner lamina is widely separated from the inner face of the outer lamina.   One specimen (PF 3851, fig. 17A) has part of the scapulo-coracoid preserved, attached to the inner face of the cleithrum near the angulation between the dorsal and ventral parts, and covering the center of radiation (fig. 18, *SC–CO*). It appears to consist of a thin layer of superficial bone covering spongy bone.   Another specimen (PF 3846, fig. 17B) shows rugosities in the area of attachment of the scapulo-coracoid. Other lungfishes, as far as is known, have cartilaginous scapulo-coracoids.

The only knowledge of the clavicles of *Uranolophus wyomingensis* comes from two specimens, PF 3851 (fig. 17A) and 5364, which preserve, respectively, the inner surface and an impression of the inner surface of the postero-dorsal part of this bone.   These show a curved blade, concave medially, with a distinct dorsal process.   The clavicle lies against the inner face of the adjacent part of the cleithrum, and

its ventral edge lies against the ridge formed by the antero-dorsal edge of the inner lamina of the cleithrum. Nothing is known of the more anterior part of the clavicle.

A single plate, PF 3865 (fig. 17D), is provisionally identified as an interclavicle. In life it was approximately symmetrical, but has been bent near the midline, flattened, and distorted somewhat. It is broadest posteriorly and narrows considerably anteriorly. Most of its outer surface is cosmine-covered, but along all but the posterior part of each lateral edge there is a broad overlap area, presumably for the clavicle; anteriorly there is a narrow area probably overlapped by a gular plate. *Neoceratodus* has an interclavicular cartilage rather than a bone, and apparently this was true of most fossil lungfishes. A probable interclavicle has been reported in *Dipterus* (Watson and Gill, 1923, p. 207; Forster–Cooper, 1937, p. 229), but it has not been described.

It would be of interest to compare the shoulder girdle of *Uranolophus* with that of *Dipterus*, but the latter is not known in sufficient detail. Later lungfishes whose shoulder girdles are well known, such as *Sagenodus*, *Ctenodus*, and *Neoceratodus*, show many differences. However, a close comparison can be made with Devonian rhipidistian crossopterygians, such as *Eusthenopteron* (Jarvik, 1944). The cleithrum of the latter can be compared point by point, and the only important difference is that it has a small ventral ridge on the inner surface instead of a strong inner lamina. The clavicle is attached in a similar fashion to the cleithrum, and has a postero-dorsal process like that of *Uranolophus*. A small, oval interclavicle is present, but *Glyptolepis* may have had a broad one more closely comparable to that of *Uranolophus* (Gross, 1936, fig. 8g). It is worth noting that Gross (1956, pp. 12–13, fig. 4) described from the Baltic Upper Devonian some shoulder girdles that are comparable to those of *Uranolophus*; he attributed them to the osteolepid, *Latvius*, but considered the possibility that they might belong to the dipnoan, *Rhinodipterus*.

Body and fins.—One of the most important specimens obtained at the Field Museum excavations in Cottonwood Canyon in the northern Bighorn Mountains is the partially articulated type specimen of *Uranolophus wyomingensis*, collected in 1962 by Dr. E. S. Richardson, Jr. Unfortunately, since the close of the 1960 field season this specimen had been lying under less than one inch of matrix, and had been subjected to severe weathering. As a result, the posterior and much of the ventral part of the body was lost, and the only fins preserved are the first dorsal and part of the second dorsal. What

is left of the body (fig. 1) suggests that it was at least as robust as that of *Dipterus valenciennesi*, as restored by Forster–Cooper (1937, fig. 1).

The position of the dorsal fins appears to be much the same as in *Dipterus*, that is, close together and far posterior on the body.   The
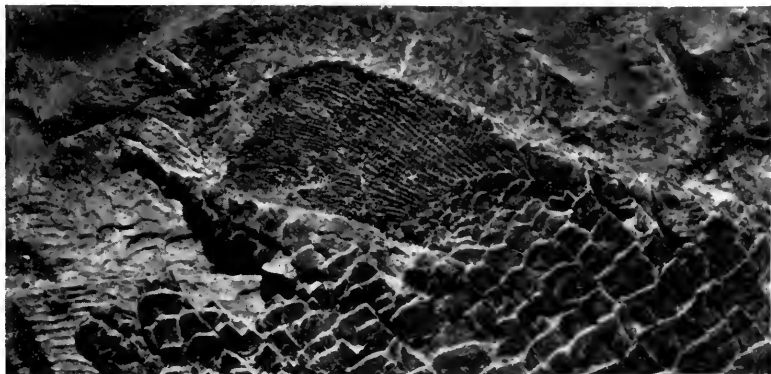

Fig. 19.   First dorsal fin and base of second dorsal fin of type specimen of *Uranolophus wyomingensis*, n. sp., PF 3874 ($\times$ 1).

first dorsal is relatively larger than in *Dipterus valenciennesi*; its length measured along its axis is approximately two-thirds of the median length of the cranial roof, while in *Dipterus* the corresponding ratio is only one-third.   The second dorsal of *U. wyomingensis* is surely larger than the first, but only part of its base is preserved. The relatively large size of the first dorsal fin is probably a primitive feature; all other lungfishes in which the dorsal fins are known, except *Rhynchodipterus*, have the first dorsal reduced, modified, or fused with the second dorsal.

The first dorsal fin (fig. 19) has at its base a small, sharply delimited lobe, presumably muscular in life; it is covered with cycloid, cosmine-coated scales which diminish in size distally, but proximally become larger and blend into the scale rows of the body.   The rest of the fin, except its anterior edge, is covered with cosmine-covered, dermal fin rays, agreeing in all respects with the lepidotrichia of other Osteichthyes.   Proximally, there is a series of elongate fin rays, exposed for a considerable length, but overlapped at their bases by the rounded scales of the basal lobe.   The rest of the rays are jointed and occasionally branched, and consist of small, rectangular, cosmine-covered elements that diminish in size distally.   Along the anterior

edge of the fin, two or three large, median dorsal scales bound the base of the fin. Further distally, the anterior edge is bounded by variably and irregularly shaped scales which are usually slightly larger than the adjacent elements of the lepidotrichia.

The second dorsal fin (fig. 19) is surely larger, has a relatively larger scale-covered lobe at its base, and a longer row of large, median dorsal scales along its anterior edge.

Uranolophus wyomingensis is, in general, comparable to *Dipterus* in its dorsal fins, but is presumably more primitive in the relatively large size of the first dorsal, in the small size of its scaled basal lobe, and in having the lepidotrichia mostly exposed and covered with cosmine. It is interesting to note that in these respects it closely approaches the conditions in early crossopterygians, such as *Porolepis* and *Gyroptychius* (Jarvik, 1959, figs. 11, 20D, pl. 2).

Scales.—*Uranolophus wyomingensis* is unique among lungfishes in having scales that, in general, have a rhombic exposed part and relatively narrow overlapped margins. In these respects it resembles the primitive crossopterygians, Osteolepididae and Porolepididae, rather than other lungfishes, which have cycloid scales with very broad overlapped areas. The scales are also thick, consisting of the same three layers as the dermal bones. Almost all of the scales in the collection that show the outer surface have the exposed part covered with cosmine. This is true of the partially articulated type specimen (PF 3874) and also of PF 3862, which preserves many associated scales and bones of a large individual. Almost all of the prepared isolated scales have well-developed cosmine, but PF 5546 (fig. 20A), which shows several scales believed to belong to one individual, has the exposed part only partially covered with cosmine. Many of the isolated scales which are exposed on the inner face may lack the cosmine layer; where this layer is absent, the exposed part has a denticulate surface which undoubtedly adheres better to the matrix than does the smooth inner surface. A cosmine-coated scale usually has a narrow anterior band of sloping-topped, dentine-covered denticles; this band lies between the cosmine and the bony overlapped area, but on the evidence of the articulated type specimen, was also overlapped by the scales anterior to it. Many of the cosmine-covered scales show Westoll lines and other growth phenomena; these will be discussed below.

The flank scales are closely comparable to those of early crossopterygians such as *Osteolepis* and *Gyroptychius* (Jarvik, 1948, fig. 28).
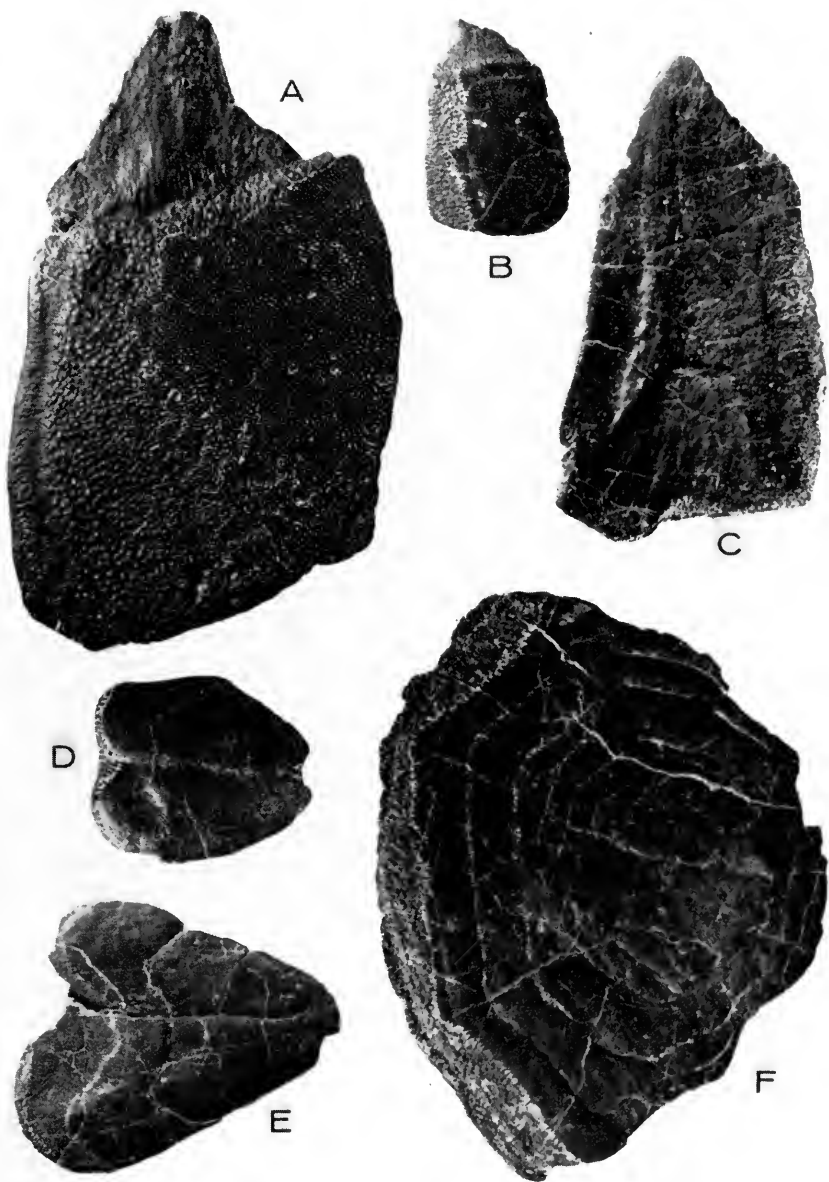
Fig. 20. Scales of *Uranolophus wyomingensis*, n. sp. (× 2). A, anterior flank scale, outer side, PF 5546; B, flank scale, outer side, PF 5548; C, anterior flank scale, inner side; PF 5547; D–F, median dorsal scales; D, PF 5544; E, PF 5545; F, PF 3862.

The exposed part is distinctly rhombic, and in the larger anterior scales (fig. 20A) the antero-dorsal to postero-ventral dimension is appreciably longer than the opposite dimension. In these scales the anterior overlapped area is narrow, but the dorsal overlapped area has a moderately to very large articular process, comparable to, but much larger than that of *Gyroptychius*. There is no groove between the exposed and overlapped areas of the outer surface, such as Jarvik (*loc. cit.*) figures in *Gyroptychius*. More posterior flank scales (fig. 20B) have the two dimensions subequal, and may have the overlapped margins broader, the articular process reduced, and the posterior angle rounded. The inner surface of the flank scales (fig. 20C) has a depressed overlap area along its posterior border and a convex depression on the ventral border for overlap of the articular process of the adjacent scale. The ridge that is characteristic of the inner face of the scales of osteolepids and porolepids is weak or absent in *Uranolophus wyomingensis*. The flank scales may reach a quite impressive size in this species. In the rather small, type specimen (PF 3874), whose total length may have been 45 cm., the largest flank scale, measured along its exposed face in an antero-dorsal to postero-ventral direction, is nearly 14 mm. long. In PF 3862, which is estimated to have been $2\frac{1}{2}$ times as long, flank scales reach at least 35 mm. in this dimension. As mentioned above, small flank scales extend onto the lobe at the base of the first dorsal fin. These are definitely cycloidal, and diminish in size distally.

Median dorsal scales are, of course, symmetrical, but show a variety of shapes. One very large one associated with PF 3862 (fig. 20F) is considerably broader than long; presumably it occupied a position close behind the head. Other relatively large ones occur a short distance in front of the first dorsal fin of PF 3874 (fig. 1); these, as better seen in isolated specimens (PF 5544-5, fig. 20D-E), are longer than broad, and taper gradually posteriorly to a rounded point. The median dorsal scales extend for a short distance up the anterior edges of the two dorsal fins (fig. 19).

Vertebral column.—A few flank scales were removed from the type specimen just behind the shoulder girdle in an effort to find the vertebral column and ribs, and a string of ossified vertebrae was revealed (fig. 21A). Each vertebra consists dorsally of a backwardly-inclined neural spine fused to a neural arch, and ventrally of a smaller element. No ribs were found. Each neural spine (fig. 21B, *nsp*) is divided along its length by a sulcus into an anterior median element, and what is probably a pair of posterior elements that overlap the
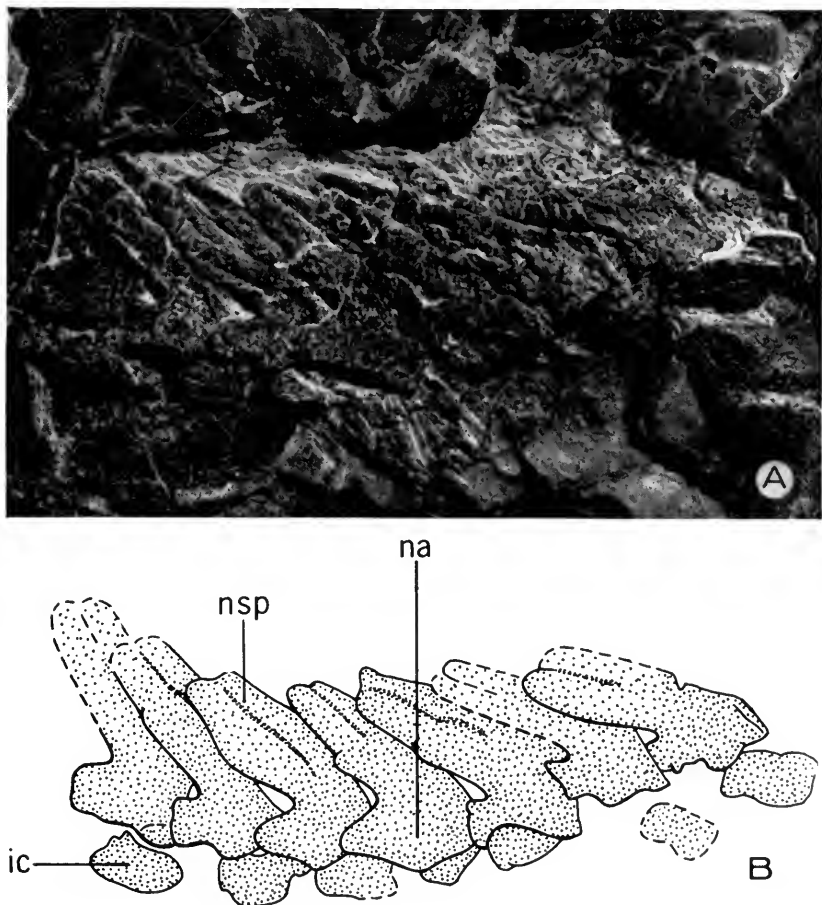
FIG. 21. Seven vertebrae of the type specimen of *Uranolophus wyomingensis*, n. sp., PF 3874 ($\times$ 2). Photograph (A) is interpreted in drawing (B). *ic*, intercentrum; *na*, neural arch; *nsp*, neural spine.

median element of the next posterior neural spine. The neural arch (fig. 21B, *na*) has a prominent process projecting posteriorly over the neural arch of the vertebra next behind. The ventral element (fig. 21B, *ic*) is probably an intercentrum, but no pleurocentrum has been recognized. The structure is basically comparable to that of living *Neoceratodus*, except that the neural arch and central elements of the latter are cartilaginous, and a small pleurocentrum is present anteriorly. It is, in general, similar to the vertebrae of *Conchopoma* (Weitzel, 1926, pp. 168–169), though in the latter the neural spines

are not fused to the arches.   There is nothing resembling the ossified, amphicoelous centra described by Jarvik (1952, pp. 40–47, figs. 16–19) in two Upper Devonian lungfishes from Greenland, and it is probable that the latter are specializations not typical of Dipnoi.

Histology.—There have been a number of studies of the histology of the dermal bones and teeth of Devonian lungfishes, especially of *Dipterus*; the most important are those of Pander (1858), Bystrow (1942), and Gross (1956, 1965).   In general, *Uranolophus* has a similar histological structure to *Dipterus* and for this reason only certain points will be discussed.

The superficial layer of *Uranolophus*, as in *Dipterus*, may consist of a continuous sheet of dentine, pierced by pore canals and underlain by mesh canals, forming the tissue known as cosmine (fig. 23C). In some individuals, or in some places, it may consist only of scattered tubercles composed of dentine (fig. 23B), and in these cases the pore-canal system must have lain in soft tissue between the denticles. In *Dipterus* and *Rhinodipterus* such tubercles are composed of bone rather than dentine (Gross, 1965, p. 122).   In scales, but usually not in skull bones, such tubercles or denticles may be overgrown and buried by bone, apparently with little resorption; new denticles or
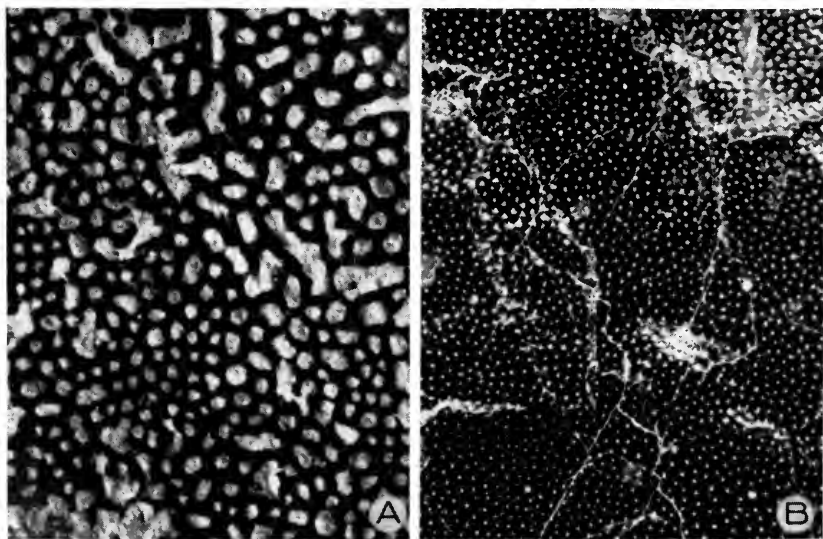

Fig. 22.   Pores of the pore-canal system on dermal plates of *Uranolophus wyomingensis*, n. sp. (× 8).   A, very large pores on undetermined plate, PF 5515; B, usual small pores, lower jaw fragment, PF 3849.

perhaps cosmine may then form on the surface, resulting in some scales in as many as four generations of buried denticles (fig. 23B–C). This type of overgrowth also occurs in some crossopterygians and actinopterygians, but has not been reported previously in lungfishes.

The pores of the pore-canal system are usually quite uniform in size on a jaw or a skull, or over all of the preserved body of the type. This is true of moderately small individuals such as the type, as well as of the largest individual in the collection (PF 3862). There is no variation clearly related to the size of the individual or to the position of the pores on the body, such as Gross (1956, p. 72) found in certain Dipteridae. In most specimens (fig. 22B) the pores range in diameter between .04 and .08 mm., approximately the same as Gross (*loc. cit.*) found most commonly in the Dipteridae he studied. There are two exceptional situations in *Uranolophus*, however. One occurs in a very small lower jaw (PF 3808), which has exceptionally large, .10 to .20 mm. in diameter, closely-spaced pores. A few isolated plates (fig. 22A) and scales have similar large, closely-spaced pores, and their smooth margins show that the pores have not been enlarged by resorption. The other unusual situation occurs in a pair of large lower jaws (PF 3797, fig. 13A) and the anterior part of a skull (PF 3805, fig. 6), which though disassociated, could well have belonged to the same individual. Here the pores of the pore-canal system are larger, .15 to .30 mm. in diameter, but are completely lacking on the anterior part of the skull and lower jaws. Two isolated snouts (PF 3848, 3868) also lack the typical pore-canal system. Sections of similar fragments (fig. 23A) show that not only the pore canals but also the mesh canals are absent. The superficial cosmine of these individuals is cut by grooves resembling sutures. On the snout of PF 3805 these grooves are similar to and continuous with sutures between the dermal bones of the middle part of the skull roof, but in a fragment (PF 3806) that has been sectioned such a groove proved to be superficial and no evidence of a suture could be found in the middle or basal layers. It is not impossible that in some cases (though probably not in PF 3805) these grooves represent a specialized remnant of the pore-canal system rather than sutures.

The pores of the lateral-line system are much larger than those of the pore-canal system, and in some cases are extremely large anteriorly. However, I do not find evidence that they had been enlarged by resorption, as indicated by White (1962, pp. 3–4) in *Rhinodipterus*. Most of the large anterior pores can be attributed to the lateral-line system, though it is not impossible that some housed specialized

sensory organs such as occur in modern dipnoans (Gross, 1956, pp. 94–96).

On the pterygoid (fig. 23F) and prearticular tooth ridges, and on the "upper lip" and dentaries (fig. 23E), the dentine becomes very thick and assumes the characteristic structure of dipnoan teeth; this consists of a type of trabecular dentine with numerous pulp canals perpendicular to the surface and many branched dentine tubules extending out from the canals. I find no evidence of a prismatic structure in this dentine, such as that described by Gross (1965, p. 128) in *Dipterus*, *Rhinodipterus*, and *Ganorhynchus*. The small denticles that cover the surface of the palate and prearticular are constructed of a simple orthodentine. The surface of the dentine is covered by a thin, transparent layer that has often been identified as enamel; however, it is penetrated by numerous dentine tubules and is more probably durodentine or enameloid, as has been shown in *Ganorhynchus* by Gross (1965, p. 124). On the tooth ridges this layer is worn off by the abrasion of chewing. On other superficial parts of the skull and jaws the enameloid and outermost dentine may be removed locally in some specimens, just as in *Cardipeltis* (Denison, 1966, pp. 111–112). This is demonstrably not the result of abrasion, and may be due either to resorption or infection.

The middle layer is spongy bone that is generally crushed in specimens from Cottonwood Canyon. It is usually rather thin, but in the snout and anterior parts of the lower jaws (fig. 23A) it becomes very thick. In scales it may include several generations of buried denticles (fig. 23B–C).

The basal layer is typically a dense, cross-laminated bone, sometimes called isopedine. During growth additional laminae are added basally, resulting often in a thick basal layer; however, on the snout and anterior parts of the lower jaws it apparently remains thin. Usually there are very few vascular canals, but one specimen (slide 5082) has in one region numerous large canals, some clearly enlarged by resorption. Scales have the usual thick layer of dense, evenly cross-laminated isopedine, which shows a very regularly alternating structure between crossed nicols (fig. 23D). At the base in cross sections there may be a bulge, which is presumably the inner ridge. The lamination is convex inward in this bulge, but between crossed nicols there appears a very distinct structure, cutting across the lamination, and sometimes resembling a secondary lamination. This cross structure indicates a distinct crystalline orientation, and presumably is the result of an original coarse fibrous structure cutting across the lamination.
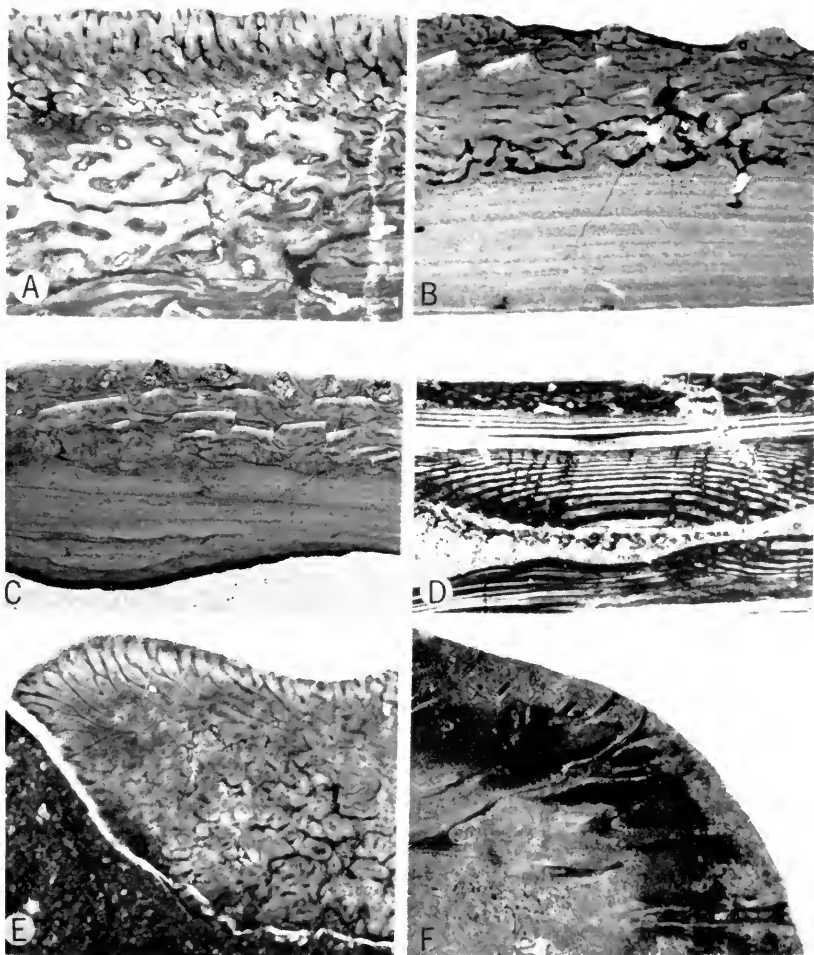
FIG. 23. Thin-sections of *Uranolophus wyomingensis*, n. sp. (A–E, × 25; F, × 75). A, longitudinal section through splenial of large lower jaw lacking pores and canals of the pore-canal system, slide 4609; B, transverse section of a scale with tuberculate surface and two generations of overgrown denticles, slide 5090; C, transverse section of a scale with cosmine surface and three or more generations of overgrown denticles, slide 4258; D, transverse section of a scale and part of another of the type specimen, PF 3874, between crossed nicols to show the lamination of the basal layer, slide 5085; E, longitudinal section through the tip of the dentary of PF 3850, slide 5088; F, transverse section through the pterygoid tooth ridge, slide 4254.

Growth of scales, skull bones and tooth ridges.—Cosmine, since it consists typically of a continuous layer of dentine, has imposed severe restrictions on the growth of those fish that possessed it. Early
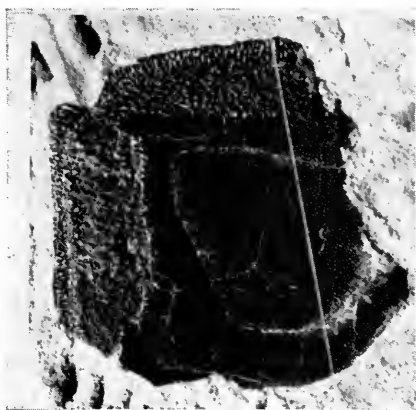

Fig. 24.   Scale of *Uranolophus wyomingensis*, PF 5541 (× 3), showing position of section illustrated in Figure 25.

Osteostraci, such as *Tremataspis*, whose carapace was completely covered by cosmine, simply did not grow after the formation of the cosmine, and presumably passed through an unarmored larval stage. The other two groups of fishes with cosmine, Dipnoi and Crossopterygii, did manage to grow by various expedients, though most of them lost cosmine quite early in their evolutionary history.   It is clear that *Uranolophus wyomingensis* overcame the cosmine problem and grew. This is shown by the considerable size range of specimens in the Field Museum collection (indicating an estimated total length of 35 to 110 cm.), by growth lines, and by histology.   Thin sections have revealed that the manner of growth was different in scales and in dermal bones of the skull roof and lower jaws, and these will be discussed separately.

Transverse sections of cosmine-coated scales (fig. 23C), often reveal several generations of dentine-capped denticles buried beneath the cosmine.   Each generation of denticles was at the surface of the scale during one stage of growth before cosmine was formed.   Detailed study of a scale in thin-section shows that the history of growth may be very complex, and that growth may continue well after the first formation of cosmine.   The sectioned scale (fig. 24), which was about 16 mm. in diameter, had a central-posterior area of cosmine,
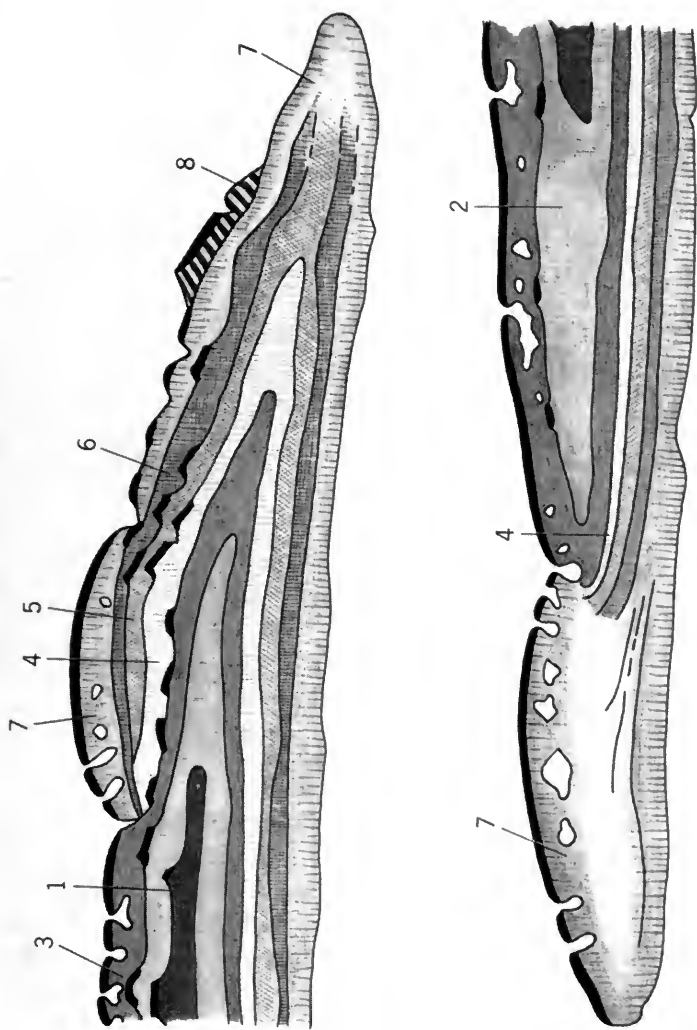
FIG. 25. Semi-diagrammatic section of the scale of *Uranolophus* shown in Figure 24. The longitudinal magnification is approximately 20 times, but for clarity some of the central part of the scale has been removed, and the vertical magnification has been exaggerated. The eight numbered stages of growth, as interpreted, are explained in the text.

separated by a Westoll line from a surrounding ring of cosmine (incomplete posteriorly where the scale was broken), and two small anterior patches of cosmine also separated by a Westoll line from the cosmine ring. In front was an overlapped area consisting only of bone most anteriorly, but capped with numerous denticles adjacent to the cosmine. As interpreted (fig. 25), the section shows two early generations of denticles (stages 1–2), overlain by the first layer of cosmine (stage 3), which forms the central-posterior area. A set of buried denticles is probably related to this generation of cosmine, and is thought to have covered part of the anterior overlapped area at this stage of growth. The next three stages (4–6) of growth are largely restricted to the anterior part of the scale, and are covered only by denticles. However, the following stage (7) involved the formation of cosmine in a ring around the exposed area of the scale, and probably also of a denticulate band in the anterior overlapped area. The final growth stage shown in the section (8) is indicated only by a small patch of bone surmounted by a single denticle near the anterior end of the scale. The third generation of cosmine was not included in this section. Though this scale shows a complicated history, it is probably simpler than larger scales with more numerous Westoll lines.

The manner of growth of *Uranolophus* scales differs from that of other lungfishes. Post-Devonian and most Upper Devonian lungfishes had completely lost the cosmine and so were not faced with the growth problems that it imposed. In *Dipterus* cosmine may be present or absent, but in spite of a number of studies it is not yet certain just how *Dipterus* scales grew. Westoll (1936, p. 169) and Forster-Cooper (1937, p. 227) showed that cosmine was periodically resorbed to permit growth. Bystrow (1942, p. 286) and Jarvik (1950, p. 39) differed as to whether resorption and regrowth was centrifugal or centripetal, then Gross (1956, p. 78) demonstrated that areas of cosmine did not grow, but were formed all at once, with finished, enameloid-coated edges. In whatever manner *Dipterus* scales grew, major amounts of cosmine resorption were involved, and cosmine did not overgrow earlier generations of cosmine or denticles. In *Uranolophus*, on the contrary, resorption played no important part in scale growth and cosmine regularly overlies older denticles, though probably not earlier layers of cosmine. In this respect it is closely similar to the primitive crossopterygian, *Porolepis*, in which one or more generations of dentine-crowned denticles are commonly buried beneath later cosmine (Gross, 1966, p. 41, fig. 5A).

Such skull bones as operculars and gulars, which did not fuse to each other or to the rest of the dermal cranium, could have grown in a similar manner to scales. Apparently they did not, however, as is shown by thin sections of small fragments of three operculars. The smallest sectioned opercular (PF 3839) has a maximum diameter of 61 mm.; its outer surface is largely tuberculate, and the surface tubercles rest on bone which has been eroded on the surface by resorption; the superficial bone layer covers one buried denticle whose crown is partly resorbed. The second opercular (PF 3835) has a maximum diameter of 71 mm.; its surface is covered with large-pored cosmine, and the section shows no buried denticles. The largest opercular (PF 3862) has a maximum diameter of 100 mm.; it has fine-pored cosmine, and the section shows no buried denticles. In these three operculars, the basal layer shows an increase in thickness in the larger plates $(0.19 - 0.39 - 0.68$ mm., respectively), but the middle and superficial layers do not, and only one denticle of an earlier generation was preserved. This suggests that there has been extensive resorption and replacement of denticles and cosmine during growth.

The growth of the plates of the cranial roof and of the ventral and lateral sides of the lower jaws of *Uranolophus* is distinctly different from that of its scales. Individual plates tend to fuse at their sutures, and the sutures are commonly overgrown by a sheet of cosmine. The relatively small type specimen (PF 3874) has many, but not all, of its cranial roof sutures covered by cosmine; where covered, they are indicated by a linearity of pore arrangement along the suture. The largest specimen, PF 3862, has similar small-pored cosmine covering the lower jaws, and no sutures are evident. Specimens of intermediate size show a variety of conditions which cannot be related in any way to size. Some have fine-pored cosmine covering many sutures. One (PF 3792) is entirely covered with denticles of dentine, except for a narrow band of cosmine at the snout. A large skull (PF 3805) has open sutures and large-pored cosmine, except on the snout where there are no pores (and presumably no canals) of the pore-canal system. A pair of lower jaws (PF 3797) is similar. Finally, another large skull (PF 3816, fig. 5) has fine-pored cosmine, Westoll lines, and areas of cosmine resorption along sutures and Westoll lines. Of the thin sections that have been made of skull or jaw plates, only one shows buried denticles, probably all of one generation; in most cases buried denticles and cosmine are definitely absent. These sections, the moderate-sized denticulate specimen (PF 3792), and the large specimen with partly resorbed cosmine (PF 3816) all indicate

that cosmine and denticle resorption was a regular process on the skull and lower jaws, and was probably extensive, as in *Dipterus.* Presumably at times when cosmine was resorbed there was an opening of sutures and a period of growth. In some cases this was followed or accompanied by the formation of dentine-capped denticles on the surfaces, while in other cases cosmine was formed again. In certain individuals there was a modification of the pore-canal system when the cosmine was absent; in some individuals this resulted in the development of large pores, and in others in the loss of the pore-canal system on the snout and anterior ends of the lower jaws.

The growth of the tooth ridges is a special problem. Since they are composed of dentine, they cannot grow on their surfaces, and since they are fused to the pterygoids and prearticulars they cannot grow at their bases. Yet they are not only longer in larger individuals, but they are also higher and wider. This may have been accomplished by a periodical resorption and reformation of the tooth ridges. One large skull (PF 3816) is at the intermediate stage in the replacement; it completely lacks tooth ridges and the margins of the pterygoids are bone, probably only partially covered by dentine. The replacement of tooth ridges is also supported by the fact that large skulls of older individuals may have tooth ridges that are relatively sharp and unworn.

Relationships.—The phylogenetic significance of *Uranolophus* will be discussed in another paper. At this time it will suffice to state that it is in most respects a very primitive lungfish, and that it may be grouped with *Dipnorhynchus sussmilchi* and *D. lehmanni* in the family Dipnorhynchidae. The latter, here characterized by similarities in cranial roof bone pattern and proportions, and by the absence of tooth plates, was originally proposed by Berg (1940, p. 385) for *Dipnorhynchus* alone. *Ganorhynchus* and *Holidipterus* may also be related, as was first suggested by Gorizdro–Kulczycka (1950, p. 95), but these genera are inadequately known. *Griphognathus* has been included by Vorobyeva and Obruchev (1964, p. 307), but is so aberrant in its slender jaws, long retro-articular process, and minute, isolated teeth that this is unlikely.

II. Lungfishes from the Water Canyon Formation
of Utah and Idaho

The Card member or lower part of the Water Canyon formation of Utah (Williams and Taylor, 1964, p. 39) has been correlated approximately with the Beartooth Butte formation on the evidence of its fish fauna. In it fragments referable to *Uranolophus* sp. have been collected at three localities in Cache County:

Blacksmith Fork, locality A (Denison, 1952, p. 266): PF 352, a small scale with cosmine coating and a marginal area with sloping denticles.

Blacksmith Fork, locality D (*loc. cit.*): PF 496, a scale with Westoll lines and denticulate margin.

Cottonwood Canyon, locality G (*op. cit.*, p. 267): PF 927, a large, median dorsal scale with Westoll lines.

An undetermined lungfish plate and scale (PF 497–8) occur also at locality G.

The Grassy Fork or upper member of the Water Canyon formation is presumably younger than the Beartooth Butte formation, and contains a distinct fish fauna that is as yet undescribed except for *Psephaspis williamsi* Ørvig (1961, p. 526) and *Protaspis erroli* Denison (1967). From the ridge south–southeast of Naomi Peak, locality H (Denison, 1952, p. 267), in Cache County has come a fragment of a snout of a small, undetermined lungfish (PF 340) which is much smaller than any referred so far to *Uranolophus*.

A few lungfish fragments have also been obtained from the lower member of the Water Canyon formation of southeastern Idaho (Coulter, 1956, p. 30). Scales (PF 5554–8, 5560), a probable antero-lateral gular (PF 5553), and an incomplete angular bone (PF 5559), all referable to *Uranolophus* sp., have been obtained from the west slope of the ridge on the east side of the North Fork of St. Charles Creek, about 6½ miles west of St. Charles, Bear Lake County. Undetermined lungfishes from this locality are skull plates (PF 5562–3) and scales (PF 5561, 5564). At a slightly higher level at this locality, but still within the lower member of the formation, has come a very

small and incomplete tooth plate (fig. 26) which may be referred to *Dipterus* sp. (PF 5566). This is of particular interest because it is the oldest known dipnoan dental plate, and shows that more conventional lungfishes existed approximately contemporaneously with
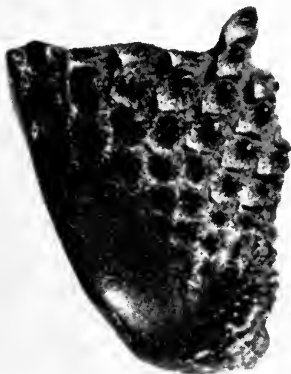

FIG. 26. Incomplete tooth plate of *Dipterus* sp. from the Water Canyon formation of southeastern Idaho, PF 5566 (× 8).

Uranolophus. It preserves parts of seven rows of denticles, and on unworn parts the individual denticles of a row are completely distinct. Each denticle is capped with shiny dentine or enameloid and separated from adjacent denticles in its own and neighboring rows by a spongy tissue, surely bone. In this respect it differs from many other *Dipterus*, in which adjacent denticles are contiguous, and resembles the presumed primitive condition shown in embryonic *Neoceratodus* (Semon, 1901, pl. 19, figs. 10–11). On worn rows or parts of rows the individual denticles are reduced to form a continuous ridge, though the position of the original denticles is indicated by swellings on the ridge. The apex of the tooth plate has been worn smooth and shows no evidence of the original rows of denticles.

Uranolophus sp. also occurs at another locality about 1 mile north of Beaver Creek along the Beaver Creek to Green Canyon Road, about 6½ miles west–southwest of St. Charles in Franklin County. From here have come flank scales with sloping denticles and Westoll lines (PF 5568) and a skull plate with lateral-line pores and Westoll lines (PF 5569).

All of these lungfish fragments have come from rocks that are probably of marine origin, though there are no diagnostically marine

invertebrates associated with them. They occur in limestones which are widespread, and locally contain *Lingula*, pelecypods, gastropods, and ostracods. Marginal marine environments have been suggested (Denison, 1956, p. 414; Williams and Taylor, 1964, p. 42), though it is not impossible that some freshwater sediments are interbedded with the marine ones.

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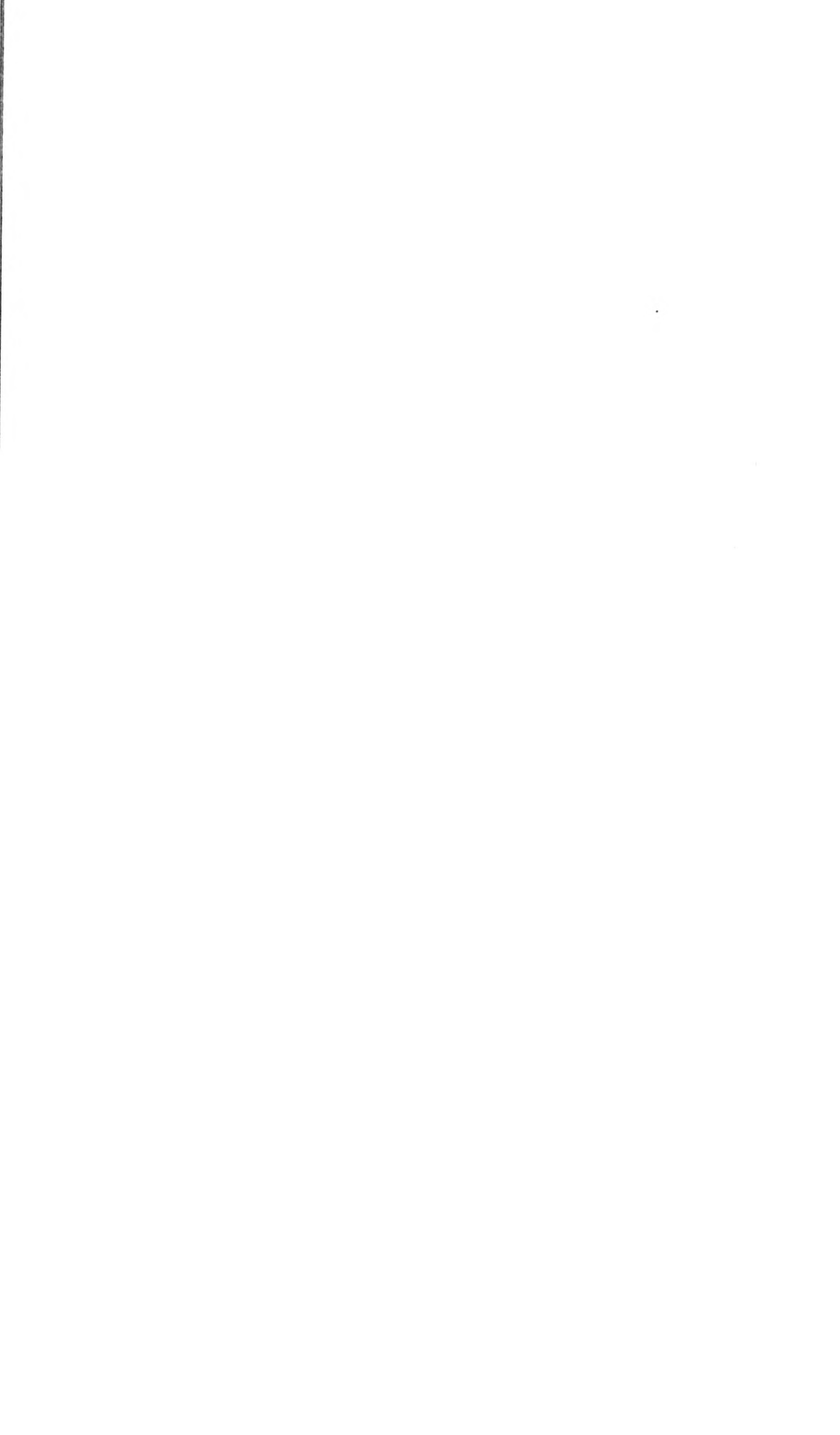
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