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The Structure and Relationships of the Primitive Devonian Lungfish—*Dipnorhynchus sussmilchi* (Etheridge)

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BULLETIN 38 • JULY 1971
PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY
NEW HAVEN, CONNECTICUT 06520

Bulletins published by the Peabody Museum of Natural History, Yale University, are numbered consecutively as independent monographs and appear at irregular intervals. Shorter papers are published at frequent intervals in the Peabody Museum *Postilla* series.

The *Peabody Museum Bulletin* incorporates the *Bulletin of the Bingham Oceanographic Collection,* which ceased independent publication after Vol. 19, Article 2 (1967).

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Printed in the United States of America

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Yale University Peabody Museum of Natural History Bulletin No. 38,
109 p., 95 figs., 1971

THE STRUCTURE AND RELATIONSHIPS OF THE PRIMITIVE DEVONIAN LUNGFISH— *Dipnorhynchus sussmilchi* (Etheridge)

Keith Stewart Thomson and K. S. W. Campbell

ABSTRACT

Dipnorhynchus sussmilchi (Etheridge) is an early Emsian-early Eifelian marine Devonian lungfish. The structure of the skull, scales, and portions of the branchial skeleton are described from acid preparations of uncrushed specimens. A detailed examination of the dermal bone patterns and the lateral-line system in *Dipnorhynchus* and comparison with other Paleozoic lungfish allows refinement of the Forster-Cooper system of bone nomenclature. New interpretations of the mandibles of *Dipterus* and *Melanognathus* together with description of the mandible in *Dipnorhynchus* are also made, with some observations on the evolution of the whole head region in Dipnoi. The endocranium of *Dipnorhynchus* is well preserved and shows important differences from that of other known Dipnoi in the oticotemporal region. A unique structure, cautiously identified as an hyomandibula, is present. The scales of *Dipnorhynchus* are extremely similar to those of *Uranolophus* and show certain resemblances to those of Crossopterygii. A new outline scheme of dipnoan evolution is derived from study of a variety of different structural complexes. It is concluded that the Dipnoi show sufficient similarity to the Crossopterygii to warrant their inclusion in a single group Sarcopterygii.

Zusammenfassung

Dipnorhynchus sussmilchi Etheridge ist ein Lungenfisch aus dem Unteren Ems-Unteren Eifel marinen Devon. Der Bau des Kopfes, die Schuppen sowie Teile des branchialen Skeletts wurden beschrieben an Hand von säurepräparierten, unzerstörten Fossilien. Durch eine genaue Untersuchung der Deckknochenanordnung und des Seitenliniensystems des *Dipnorhynchus* im Vergleich mit anderen paläozonischen Lungenfischen wurde es möglich, das Forster-Cooper System der Knockennomenklatur genauer zu definieren. Auch wurden neue Deutungen der Mandibeln von *Dipterus* und *Melanognathus* gemacht sowie eine Beschreibung des Mandibels von *Dipnorhynchus* und einige Bemerkungen zur Evolution der ganzen Kopfregion der Dipnoi. Das Endocranium des *Dipnorhychus* ist gut erhalten und weist wichtige Unterschiede auf im Vergleich mit anderen bekannten Dipnoi in der Otico-Temporal Region. Bemerkenswert ist eine Struktur, die wir hier vorsichtshalber als Hyomandibulare bezeichnen. Die Schuppen des *Dipnorhynchus* sind denen des *Uranolophus* äusserst ähnlich und zeigen auch gewisse Ahnlichkeiten mit denen der Crossopterygii. Eine neue Evolutionstheorie für die Dipnoi basiert auf Untersuchungen einer Anzahl verschiedener Gruppen morphologischer Merkmale. Wir sind der Meinung, dass die Dipnoi genügende Ahnlichkeiten mit den Crossopterygii haben, um sie als selbständige Gruppe Sarcopterygii einzureihen.

РЕЗЮМЕ

Dipnorhynchus sussmilchi Этридж — морская девонская двоякодышащая рыба ранне-эмского или ранне-эйфельского периодов. Структура черепа, чешуи и костяка жабры описаны по кислотным препаратам цельных образцов. Детальное исследование структуры дермальных костей и системы боковых линий у *Dipnorhynchus* и сравнение с другими палеозойскими двоякодышащими рыбами позволяет уточнить систему костяной номенклатуры Форстера-Купера. Приводятся новые интерпретации нижней челюсти у *Dipterus* и *Melanognathus,* а также и описание нижной челюсти у *Dipnorhynchus* с некоторыми наблюдениями об эволюции всей головной области двоякодышащих. Эндокраниум у *Dipnorhynchus* хорошо сохранился и свидетельствует о значительном различии в ушно-височной области между ним и другими известными двоякодышащими. У *Dipnorhynchus* здесь находится единственная в своем роде структура, предварительно определяемая, как гиомандибула. Чешуя у *Dipnorhynchus* очень похожа на чешую *Uranolophus* и имеет некоторое сходство с чешуей группы Crossopterygii. Новая схема эволюции двоякодышащих выводится из исследования различных структуральных комплексов. В заключение констатируется, что сходство двоякодышащих с группой Crossopterygii достаточно велико, чтобы включить их в единую категорию Sarcopterygii.

INTRODUCTION

The lungfishes (Osteichthyes: Dipnoi) have long occupied a special place in the study of evolution. It is well known that the fossil record of the group extends from the Devonian to the Quaternary and that the three living genera are in many ways "living fossils," being little changed from their Mesozoic ancestors. The continuity of the fossil record of Dipnoi has made them ideal subjects for the study of modes and rates of evolution. However, the Dipnoi are of more general importance because of their close anatomical similarity to the Amphibia. When first discovered, they were described as amphibians—a misapprehension soon corrected by Huxley and Lankester. However, the presence of lungs, used in obligate air-breathing in *Protopterus* Owen and *Lepidosiren* Fitzinger, the lobed-paired fins and the structure of the heart and brain, among other features, persuaded many that the Dipnoi constituted the ancestral stock from which tetrapods had evolved. Later the position of honor had to be yielded to the Paleozoic Crossopterygii (specifically the Rhipidistia) and since that time the problem of the precise phylogenetic position of the Dipnoi has been the subject of considerable discussion. As will be noted below, the Dipnoi have normally been closely linked with the Crossopterygii, but this has been contested in recent years. Therefore, whereas the Dipnoi are one of the best-known groups of fishes, many important problems concerning their history remain to be solved.

Recently, due to certain important discoveries, attention has been concentrated on the very early history of the Dipnoi. Up to 1945, the earliest known fossil dipnoan was *Dipnorhynchus sussmilchi* (Etheridge) from the Early to Middle Devonian of Australia. This species was represented by a specimen showing the skull roof and a poorly defined lower jaw (Etheridge, 1906; Hills, 1933, 1936, 1941). In 1945, Lehmann discovered a specimen in the Hunsrückschiefer of Germany that was later described (Lehmann and Westoll, 1952; Lehmann, 1956) as *Dipnorhynchus lehmanni.* This specimen showed the skull roof and part of the palate, although the preservation made the identification of many details uncertain (see later discussion). In 1963, H. A. Toombs of the British Museum (Natural History) collected a detached palate, an almost complete lower jaw, and a second jaw fragment of *D. sussmilchi* in the area from which the holotype had been collected. In 1964, K. S. W. Campbell discovered a second specimen of the skull of *D. sussmilchi* that showed a very well-preserved skull roof and palate. A preliminary description of this specimen was published (Campbell, 1965), and full-scale preparation of the new specimen was started as a prelude to the present more comprehensive treatment. In addition, it was realized that the holotype could also be prepared to show further structures. Ultimately, all the materials of *D. sussmilchi* were assembled by the present authors and prepared. All were found to be essentially uncrushed and preserved in a most remarkably detailed way.

In 1968, Denison (1968a,b) published a description of a new Lower Devonian from *Uranolophus* from the western United States. Although slightly less well preserved in the cranial region than *Dipnorhynchus sussmilchi,* this material has provided extremely important new information concerning the postcranial skeleton of a primitive lungfish.

We present, in the following account, a description of the structure of *Dipnorhynchus* and a reassessment of dipnoan morphology and relationships based on a comparative study of early Dipnoi. In the authorship of this paper, Campbell was largely responsible for the sections involving the skull roof and jaw and Thomson for the braincase and palate. The final version is our joint work.

ACKNOWLEDGEMENTS

This study has been made possible by the assistance and support of a large number of individuals and institutions to whom we acknowledge our thanks. We are grateful to Dr. E. I. White [British Museum (Natural History)], Mr. E. D. Gill (National Museum, Melbourne), Mr. H. O. Fletcher (Australian Museum, Sydney), Dr. J. A. Warren (Monash University, Melbourne), Dr. R. S. Miles (Royal Scottish Museum, Edinburgh) and Dr. D. Russell (National Museum of Canada, Ottawa) for the loan of specimens. The material was prepared by Messrs. H. A. Toombs and C. I. Macadie [British Museum (Natural History)] and J. Bein (Australian National University) upon whose skill much has rested. The drawings and drafting work were performed by Mrs. Judy Davis and Mrs. Robin Lawrie (Australian National University) and Miss Ward Whittington and Miss Diane McClure (Yale University). Photography was done by Mr. L. Seeuwen (Australian National University) and Mr. A. H. Coleman (Yale University). Dr. M. G. Pinner (Canberra) very kindly gave of her time to make the X-ray pictures; the preparation of these into positive plates was made possible through the generous assistance of Dr. Rainer Zangerl (Field Museum of Natural History, Chicago). Dr. R. H. Denison and Professor E. Jarvik very kindly gave us advance copies of their recent papers. We are grateful to Dr. E. I. White, Dr. R. S. Miles, Dr. S. M. Andrews, Dr. R. Barwick, Dr. H. Fox, and Dr. Denison for valuable discussions in the course of the preparation of this paper, and to Professor D. A. Brown (Department of Geology, Australian National University) for his encouragement and generous provision of facilities. The work has been supported in part by grants GB 4814 and GB 7573X from the National Science Foundation to Thomson, who was also an Honorary Research Fellow of the Australian National University for part of 1967. Campbell's contribution has been supported by research funds from the Australian National University. This Bulletin has been published with the aid of NSF grant GN–528.

MATERIALS AND METHODS

With one exception, the material used in this study has come from the Lower to Middle Devonian limestones of the Taemas district, about thirty miles northwest of Canberra, Australia. The exception is from Buchan in northeastern Victoria, where there outcrops a sequence of rocks similar in lithology, faunal content, and age to those at Taemas (see later discussion).

The first specimen to be described (the holotype, Australian Museum AM F10813A, Etheridge, 1906) was collected by G. A. Sussmilch from a locality given as Portion 44, Parish of Taemas. Browne (1959), however, records that the specimen came from the *Spinella yassensis* Limestone outcrop less than half a mile north of Taemas house. It is not known if it was found loose or *in situ.* The holotype, which was taken to be a skull roof and snout only, was redescribed by Hills (1933, 1941) who, although he did not seek to extract it from the matrix, prepared the lateral-line system on the left side of the skull roof. A small fragment of bone (AM F10813B) in the matrix on the undersurface of the specimen was interpreted as an isolated tooth plate. Through the courtesy of H. O. Fletcher, Curator of Fossils at the Australian Museum, permission was obtained in 1967 to prepare the specimen by acid etching in the Department of Geology, Australian National University. This work was done by J. Bein, using techniques based on those developed in the British Museum (Natural History) by H. A. Toombs and A. E. Rixon (see Toombs, 1959 and Rixon, 1949, for details). It revealed a superbly preserved palate and braincase in almost the natural position beneath the skull roof.

In 1936 Hills described the external dermal bones of a mandible from Buchan, Victoria, as a probable representative of *Dipnorhynchus.* A large part of the external surface had been lost before it came to the National Museum, Melbourne, where it is now housed (P 13837). However, interpretation was possible because an impression of the radiating structure of the internal surfaces of the dermal bones had been left on the matrix filling the Meckelian vacuity. Permission was obtained from E. D. Gill, Deputy Director of the National Museum, to prepare this specimen by acid etching after the above-mentioned structures had been recorded in plaster casts. Not only were the internal elements of the mandible found to be almost complete and uncrushed, but the cavities of the jaw contained a large cheek plate (P 13837A, National Museum), several scales (P 13837B-F), and a portion of the branchial apparatus (P 13837G). Neither the exact locality nor horizon of this specimen is known. Attempts to identify the horizon by recovering microfossils from the acid residues were unsuccessful.

In 1963, Toombs visited the Taemas area and collected three specimens in loose rocks; because of the nature of the weathering and topography it is possible to fix their provenance within narrow limits. These specimens were all prepared by acid etching in the British Museum (Natural History) and are now in the collections of that institution. The first specimen (P 33699) is the greater part of a palate with a detached snout, from the Bloomfield or *Receptaculites* Limestones about ½ mile west-southwest of Taemas Bridge. It is undescribed, but White (1965, p. 36) referred to the character of its dentition. The other two specimens are mandibles. One (P 46773) is almost complete, lacking only some of the dermal bone on the left side. It was found on the right bank of the Burrinjuck Dam, 2,500 yards east of Majurgong trig., and is almost certainly from the *Spinella yassensis* Limestone. The other specimen (P 33714) was found approximately 1,950 yards on a bearing 352° magnetic from the Bloomfield Homestead and is probably from the Bloomfield Limestone. Both of these mandibles were mentioned by White (1965, p. 39) and P 33714 was sectioned to provide the histological data given by that author in a more recent paper (White, 1966; p. 7, pl. 1, fig. 1).

Isolated scales from the same area were collected by J. A. Warren, Monash University (1970D and thin-section 2931—Zoology Department Collections).

In 1965 an almost complete skull was discovered at the locality known as Shearsby's Wallpaper, Taemas, in the *Spinella yassensis* Limestone (see Campbell, 1965). This specimen has also been etched in acid. The braincase is less complete posteriorly than that of the holotype, but the skull roof is almost entire. It is now cataloged as 18815 in the Geology Department Collection, Australian National University. These specimens are illustrated in Figures 1 to 35 and in numerous photographs (Figures 36 to 95).

acv	anterior cerebral vein
alc	anterolateral chamber of nasal organ
amc	anteromedian chamber of nasal organ
amt	anteromedian tuberosity
an	position of anterior naris
ang	angular
ant f	anterior furrow
ant pt	anterior pterygoid
aoa	anterior ophthalmic artery
art	articular
bb 1, bb 2	basibranchials 1, 2
c b VII	canal for n. buccalis VII
c ea I	canal for first efferent branchial artery
c ep	cavum epiptericum
c hy VII	canal for r. hyomandibularis VII
c int ca	canal for internal carotid artery
c j	canal for jugular vein
c m V (cc m V)	canals for r. maxillaris V
c mcv	canal for median cerebral vein
c o a	canal for orbital artery
c oph a	canal for anterior ophthalmic artery
c os VII	canal for r. ophthalmicus superficialis VII
c ot VII	canal for r. oticus VII
c pal a	canal for palatal artery
c pal VII	canal for r. palatinus VII
c pit v	canal for pituitary vein
c prf	canal for r. profundus V
c II	canal for optic nerve
c III	canal for third cranial nerve
cc	canals in dermal bone
cer md lig	insertion of ceratomandibular ligament
ch	vascular chamber posterior to Meckelian vacuity
cor	coronoids
d	dentary
dl cr	dorsolateral crista
dm cr	dorsomedian crista
f ch	foramen in posterior wall of Meckelian vacuity
f_1 ea—f_2 ea I	foramina for first efferent branchial artery
f int V	foramen for r. mandibularis internus V
f m ll	foramen for mandibular lateral line
f md V	foramen for mandibularis V
f me VII	foramen for r. mentalis externus VII
f_1 mi VII—f_2 mi VII	foramina for r. mentalis internus VII
f o a	foramen for orbital artery

f o ll	foramen for oral lateral line
f oph a	foramen for ophthalmic artery
f pal VII	foramen for r. palatinus VII
f prf	foramen for r. profundus V
f_1 sa I–f_2 sa I	foramina for superior branch of first efferent branchial artery
fv?	possible vascular foramina
g pr	process for m. geniocoracoideus
gl	glenoid fossa
gr ea I	groove for first efferent branchial artery
gr int ca	groove for internal carotid artery
gr j	groove for jugular vein
gr l	groove for lateral aorta
gr m V + VII	groove for r. mandibularis V and VII
gr me VII	groove for r. mandibularis externus VII
gr mi VII	groove for r. mentalis internus VII
gr subn v	groove for subnasal vein
hb 4, hb 5	hypobranchials 4 and 5
hy VII	(canal for) r. hyomandibularis VII
hyp	cavity for hypophysis
hyp r	hypophysial recess
int ca	(canal for) internal carotid artery
int pr	process for intermandibularis muscle
l p lr	lateral palatal process
lab p	labial pit
lgr	lateral groove (palate)
lr	lateral ridge (palate)
lt	lateral tuberosity (palate)
Mck b	Meckelian bone
Mck f	Meckelian fossa
Mck v	Meckelian vacuity
mcv	medial cerebral vein
mll	mandibular lateral-line canal
mm V	foramen for combined rami maxillaris-mandibularis V
mtd	median transverse depression (palate)
mv	maxillaris ramus of fifth nerve
nch	notochord
oll	oral lateral-line canal
op	operculum
op pr	opercular process of hyomandibula
ot VII	(canal for) r. oticus VII
p c	posterior chamber of nasal cavity
p md l	shelf for palatomandibular ligament
p n	position of posterior naris
p st	stalk of parietal organ
pch	"parachordal"

pit v	(canal for) pituitary vein
pmel	posteromedian elevation (palate)
pn w	postnasal wall
pr art	prearticular
pra t	prearticular tubercle
prf V	(canal for) r. profundus V
prg p	preglenoid process
psp	postsplenial
r	ridge
r a mm	ridge for adductor mandibulae muscles
r os VII	r. ophthalmicus superficialis VII
s n	solum nasi
sang	surangular
sa I	groove for superior branch of first efferent branchial artery
sl	sulcus
sp	splenial
sp r	spiracular recess
t p	tooth plate
tt	rostral tubuli (schematized in Figs. 21, 22)
uh	urohyal
vc?	unidentified vascular canals
II	foramen for optic nerve
III	foramen for third cranial nerve
IV	foramen for fourth cranial nerve
X (IX)	foramina for tenth cranial nerve

ENVIRONMENT OF *DIPNORHYNCHUS SUSSMILCHI*

All known specimens of *Dipnorhynchus sussmilchi* have been found in marine limestones and associated with an abundant and diverse fauna of brachiopods, corals, bivalves, nautiloids, polyzoans, etc.

Hills (1941) and Campbell (1965) concluded that the fish were marine, but several people have questioned this in discussion and suggested that they were carried in by streams. This matter requires examination because of its physiological and phylogenetic implications, especially as the only other known species of the genus, *D. lehmanni,* was also recovered from a marine formation, the Hunsrückschiefer of Germany.

Dipnorhynchus is not the only fish to occur in the Buchan, Taemas, and Wee Jasper limestones. There are several species of placoderms, of which the arthrodires *Williamsaspis bedfordi* White, *Buchanosteus murrumbidgeensis* White, *Taemasosteus novaustrocambricus* White and *Notopetalichthys hillsi* Woodward are the only ones described (White, 1952).

At Taemas, dermal bones of these fishes have been found in every unit from the Cavan Bluff Limestone to the Warroo Limestone, with the exception of the Majurgong Shale. They are not common and usually occur randomly distributed, but occasionally one finds relatively thin limestone units in which they are more abundant than normal; for example, at places in the Warroo Limestone, and at Cave Flat, near Burrinjuck, where about 70 completely or partly disarticulated fragments of dermal shields were collected in an outcrop 100 yards long and 20 feet thick. In this latter outcrop a well-preserved dipnoan skull was also collected, together with two small fragments of dipnoan bone. The bones are usually separated by at least several meters, never show signs of having been washed together, and are randomly oriented.

Although the placoderm shields are invariably partly or completely disarticulated and the dipnoan skulls have lost their cheek plates, the remains show little or no signs of physical transport. The surface detail is well preserved and there is little or no abrasion. This, together with the type of distribution mentioned above, suggests that the disarticulation is more likely to be the result of predation. The predators could be either large nautiloids, the remains of which are common, or the arthrodires, or both.

This interpretation of little transport is supported both by the character of the enclosing sediments themselves and by the preservation of the associated invertebrates. The specimen from Shearsby's Wallpaper came from a bed containing a profusion of the brachiopods ?*Protochonetes culleni* (Dun) and *Spinella yassensis* (de Koninck), most of which retain their valves articulated, and many of which are either in living position or just rolled over. The finest of details are preserved—for example, the cardinal spines on the chonetids and the microscopic spinules that cover both valves of the spiriferids. An assemblage of this sort requires conditions too quiet to permit the transport of a *Dipnorhynchus* skull along the sea bottom. Other specimens come from sediments indicative of rather more turbulent conditions, but in general all occurrences could be categorized as being in low-energy environments. It is quite unrealistic, therefore, to suggest that these fossils were washed in as skeletons.

However, none of the above arguments precludes the possibility that the fish were washed in alive or as bloated cadavers by rivers in floods, that they were predated in the sea with their remains falling to the bottom to be moved slightly by bottom currents before final burial. The following points can be urged against this view:

1) The limestones usually contain less than five percent of terrigenous material. On solution in acid they produce only silicified fossils and a black organic sludge, which is usually free of silt. It is true that in the *Spinella yassensis* Limestone there are numerous thin interbeds of silt and mud, which are probably of terrigenous origin, but the fish remains are in the limestone rather than in the silty sediments.

2) The associated marine fauna is rich and diversified. Many of the fish plates come from beds rich in well-preserved corals, stromatoporoids, articulate brachiopods, and fenestellid polyzoans—all of which were sensitive to turbidity and low salinity. One would expect that streams bringing in heavily armored fishes would also carry quantities of mud and be of sufficient volume to lower the salinity considerably.

3) Algae are common throughout the limestones and must have made an important contribution to their bulk. These and the associated fauna indicate a shallow-water marine platform environment.

All these features suggest that any streams debouching into the area from possible neighboring land must have been carried in very narrow channels across the limestone flats, or had very low discharge rates, or both. To date no such channels have been recognized. In the unlikely event of fish being brought down such channels and spread out from them by predators or by swimming before they died, there should be some evidence of other floating debris from the land. Vascular plants, for example, were in existence at this time as is proved by their occurrence in the Kirawin Shale, lower in the sequence in the Taemas-Wee Jasper region; yet they are very rare or absent from the limestones. In assessing the probability of such a mechanism for introducing the fish, it must be kept in mind that Buchan is about 180 miles south of Burrinjuck, which is 15 miles west of Taemas, and that it is not only one but some hundreds of occurrences of fish remains at several stratigraphic levels that have to be accounted for.

Finally, the anatomy of *D. sussmilchi* itself argues in favor of a marine origin. Its "teeth" consist of three bulbous masses anteriorly and a pair of large almost flat palatines, in addition to which the lateral edges of the palate moved against the rounded edges of the prearticulars. There are no sharp teeth that could hold struggling prey. The palate itself is very thick and to judge from the areas of insertion the adductor mandibulae must have been very large. These features taken in conjunction suggest a diet of passive (or dead) but well-protected epifaunal organisms that had to be cracked open and crushed to extract the soft body. Brachiopods, bivalves, gastropods (or possibly dead placoderms) fit these specifications admirably, and they occur in abundance in most of the fish-bearing strata. On the other hand, no such invertebrates are known to occur in Devonian freshwater sediments though freshwater placoderms of this age are known elsewhere in the world.

The balance of evidence indicates that a marine origin for the fish fauna, including *D. sussmilchi,* seems much more probable than a nonmarine origin.

AGE OF THE SPECIMENS

The limestones in all three areas from which specimens were obtained have, until recently, been regarded as either late Early Devonian or early Middle Devonian. Hill (1941), working with corals, concluded that the Cavan Bluff Limestone was probably "somewhere near the base of the Couvinian, or perhaps the top of the Coblenzian." Hills (1941) used this determination in his paper on *Dipnorhynchus.* In 1951, Hill again using corals, concluded that the Buchan Caves Limestone fauna was "near the junction between the Emsian and Couvinian, probably Couvinian." The later units at Buchan were regarded as definitely Couvinian. On the basis of ammonoid and bactritid studies Teichert (1948) concluded that the Taravale Mudstone at Buchan was Eifelian in age, thus apparently confirming the work of Hill. These determinations were accepted by Browne (1959) and Teichert and Talent (1959) in their revisions of the stratigraphy of the Murrumbidgee and Buchan areas and were only slightly modified by Talent (1965b) and Brown, Campbell, and Crook (1968) in surveys of regional stratigraphy.

In a long series of papers Philip and Pedder (1964, 1967b, 1968), Pedder (1964, 1968), Philip (1966), Philip and Jackson (1967), and Pedder, Jackson, and Philip (1970) have disputed this interpretation, largely on the basis of a restudy of the corals by Pedder and an examination of the conodonts by Philip and Jackson. Their work has been accepted without comment by two workers on the vertebrates from these areas (White, 1965; Schultze, 1968), the one quoting a Siegenian and the other a late Emsian age for the same rocks, as a result of the relatively rapid evolution of the views of these authors. A brief review of the present position is therefore warranted, especially as Philip and Pedder, even in their latest work (1968, p. 1027), cite the occurrence of *Dipnorhynchus* as evidence of a Siegenian age.

Certain warnings need to be sounded. High precision correlation of the rocks in the interval at issue is not straightforward. The faunas of the upper Emsian are, in general, more closely related to those of the Eifelian than the lower Emsian, making the definition of the Emsian-Eifelian boundary difficult. Ammonoids, which have been widely regarded as reliable age indices, are rare and little differentiated. Conodonts, which give promise of more refined correlations, remain to be adequately tested and seem to show marked provincialism. For example, icriodids, which are abundant in the northern hemisphere at this time and are used for zonation, are very rare in eastern Australia. Further, species that were thought to be reliable guides are now appearing out of sequence even in adjacent regions; for example, compare the range zones of *Spathognathodus bidentatus* and *Polygnathus kockeliana* in the Harz and Couvin areas (Wittekindt, 1965; Bultynck, 1968).

In addition, there are local facies and biogeographic problems peculiar to southeastern Australia, particularly in connection with coral distribution. For example, *Calceola* occurs in abundance at Bindi in limestones equivalent to the top of the

Buchan Caves Limestone and lower Taravale Formation at Buchan, only 35 miles distant. Yet despite the fact that the facies and the brachiopod faunas are similar, *Calceola* is apparently absent from Buchan. Such examples could be multiplied. In the light of such facts, it would be most remarkable if the Lower-Middle Devonian boundary could be precisely fixed in most sections in eastern Australia at the present time.

As shown above, most of the dipnoans come from the *Spinella yassensis* Limestone to the *Receptaculites* Limestone equivalents. The scales found by Warren are most probably from the Cavan Bluff Limestone. The horizon at Buchan is unknown. The best approach to the discussion of the age of the dipnoans therefore seems to be to examine the limits within which they can be dated.

Most workers would now accept that the Cavan Bluff Limestone is the oldest unit involved. The fauna described from it is sparse and largely endemic. It was reviewed by Philip and Pedder (1968, p. 1032). The only corals also known overseas are *Embolophyllum* and *Tipheophyllum*. According to Pedder the former genus is known elsewhere only from the Keyser Limestone of Gedinnian? age in Maryland where it is represented by a species remote from *Embolophyllum aequiseptatum* (Hill), the Cavan species. *Tipheophyllum bartrumi* (Allan) from Cavan, however, is known also from New Zealand in the Reefton Limestone that lies above the late Siegenian or early Emsian Reefton Mudstone (Boucot et al., 1963). The only other species relevant to the present discussion is the conodont *Polygnathus linguiformis dehiscens* Philip and Jackson. Out of Australia *P. linguiformis* is not known below the Emsian, but Philip and Jackson (1967) regard their subspecies as primitive and therefore indicative of a possible Siegenian age. This evolutionary argument awaits stratigraphic confirmation. The similarity between *P. linguiformis dehiscens* and *P. lenzi* Klapper (1969) from what is regarded as lower (but not basal) Emsian of the Yukon and Nevada suggests that confirmation is unlikely. We conclude that no compelling evidence has yet been put forward favoring a pre-Emsian age for the Cavan Bluff Limestone.

The oldest fossiliferous rocks at Buchan belong to the Buchan Caves Limestone. Philip (1966) regarded them as probably late Siegenian in age because they lacked *Polygnathus linguiformis,* though Philip and Pedder (1967b, 1968) later qualified this opinion, pointing to the difficulty of recognizing the Siegen-Ems boundary in Australia. The Buchan Caves Limestone contains the *Chalcidophyllum recessum* Fauna, which also occurs in the Currajong Limestone in the Taemas area, some 400 feet above the Cavan Bluff Limestone. The Buchan Caves Limestone is unlikely therefore to be older than early Emsian if the above argument is correct. The *Chalcidophyllum recessum* Fauna contains no described elements that are useful for worldwide correlation. However, the beds overlying it apparently without a break at Buchan, the Pyramids Member of the Taravale Mudstone, contain the bactritid and ammonoid faunas originally described by Teichert (1948). The reviews of bactritid and ammonoid distribution in the Lower Devonian throughout the world by Erben (1953, 1960, 1964, 1965) have shown that it is difficult to use the bactritids for fine stratigraphic correlation, and that *Teicherticeras* encompasses a group of species with a wide morphological range. The Buchan species *T. desideratum* (Teichert), *T.* sp. *D* Erben and *T.* sp. *E* Erben do not resemble the late Siegenian or early Emsian species elsewhere. On the contrary, the little evidence available suggests that the greatest similarities in coiling, whorl profile, ornament pattern, and suture shape are with species like *T. lissovi* Bogoslovskiy, the age of which is regarded as late Emsian on the basis of the associated ammonoids (Bogoslovskiy, 1963). In addition, *Talenticeras* is regarded by Erben as an offshoot from *Mimosphinctes,* showing regressive tendencies. However, he was under the impression that the local succession indicated an Eifelian age. This line of argument, like that concerning the Siegenian age of *Polygnathus linguiformis dehiscens* Philip and Jackson, is weak and in need of stratigraphic support. At present the ammonoids seemingly cannot be used to give a precise date, but the weight of evidence is against the view that the *Teicherticeras*-bearing beds of the Taravale Formation are basal Emsian as indicated by Philip and Pedder (1967b, p. 235 and text-fig. 1) or "early, though not necessarily earliest, Emsian" (Philip and Pedder, 1968). The underlying Buchan Caves Limestone cannot be dropped into the Siegenian on this ammonoid evidence.

The occurrence at Bindi of *Calceola sandalina* in abundance with brachiopods of the same type as those occurring with the ammonoids at Buchan supports this view. *C. sandalina* has not been reliably reported from pre-upper Emsian strata anywhere overseas, the oldest occurrence being in the Chapel Limestone of the Zlichovian in Czechoslovakia (Strusz, 1970). Recently Hill and Jell (1969b) have referred *Rhizophyllum calceoloides* Talent from the Kilgower Member of the Tabberabbera Formation in Victoria to *Calceola.* The Kilgower Member has been dated as probably Emsian by Talent, but is considered to be more probably middle Siegenian by Philip and Pedder (1968). However, *C. calceoloides* is acknowledged to have several characters atypical of the genus (see also Talent, 1963); Hill and Jell note that forms with similar morphology occur in the Eifelian *Calceola* beds of the Urals and in the ?Emsian of North Queensland. It seems most reasonable to conclude that the Buchan Caves Limestone can be no older than early Emsian and is more likely to be no older than the middle part of the Emsian. The absence of *Polygnathus* is to be explained either by facies or by incomplete sampling or both. Only three of Philip's samples contained conodonts, and one of these yielded just one specimen.

The youngest rocks containing dipnoans belong to the *Xystriphyllum mitchelli* Fauna of Philip and Pedder (1967b). In its characteristic development this fauna lies above the *Teicherticeras*-bearing beds at Buchan, though there is apparently some overlap in range; it appears about 400 feet above the *Chalcidophyllum recessum* Fauna at Taemas. It contains one of the richest invertebrate faunas in the region. Among the nonendemic corals there are few genera that are not long ranging. None demands an Early Devonian age but, as has been pointed out, the presence of *Acanthophyllum* suggests that it cannot be older than late Emsian (Philip and Pedder, 1967b, p. 235; 1968, p. 1032). The brachiopods *"Spirifer" yassensis, "Nadiastrophia," Cymostrophia,* and *Mutationella* have been cited as indicating an Early Devonian age (Philip and Pedder, 1964). *"S." yassensis* is a species of the Emsian to Eifelian genus *Spinella* Talent and is not closely related to the Early Devonian New Zealand genus *Mauispirifer.* The *"Nadiastrophia"* is presumably *Malurostrophia* Campbell and Talent, which is represented by several species in Victoria and New South Wales, and in the Eifelian or possibly late Emsian Ukalunda Beds of Queensland (Campbell and Talent, 1967). It is unknown out of Australia. *Cymostrophia* is not a Lower Devonian index, representatives being found in the Eifelian in the USSR in the Salair Range and the Altai Mountains, and in North America. B. D. E. Chatterton of the Australian National University, who has been studying the brachiopod and trilobite faunas of the *Receptaculites* and Warroo Limestones, informs us that he has been unable to find species of *Mutationella,* though other closely related terebratuloids are present. It is true that the occurrence of a species of *Parachonetes* Johnson close to *P. macrostriatus* (Walcott) suggests a late Emsian age, but against this must be weighed *Quadrithyrina* Havlíček, which is known only from the Eifelian of Czechoslovakia and the Urals; *Spinulicosta* Nalivkin, the only Lower Devonian occurrence of which is in the late Emsian of Nevada (Johnson, 1968) but which occurs in abundance in both Asia and America in the Middle Devonian; and *Cyrtinopsis* Scupin which ranges from the Gedinnian to the Givetian, but is represented at Taemas by a species similar to the late Emsian-Eifelian *C. undosus* (Scheer) and *C. undosus maiderensis* Drot from the Eifelian of Morocco. None of the other brachiopods being studied is limited to the Lower Devonian. We conclude therefore that the members of this group are a mixture of late Emsian and Eifelian forms, and that it would not be unreasonable to suggest on the basis of this evidence that the *Xystriphyllum mitchelli* Fauna crosses the Emsian-Eifelian boundary.

The trilobites give little indication of age. *Acanthopyge (Mephiarges) bifida* Edgell is clearly related to *A.* (*M.*) *mephisto* Richter and Richter from the Eifelian, but is just as close to *A.* (*M.*) *consanguinea* Clarke from the Gedinnian. A species of *Phacops* is at a similar evolutionary level to members of the *Phacops fecundus degener* group that ranges from the late Emsian to the early Eifelian. The occurrence of *Gravicalymene* may be thought to indicate an Early Devonian age, but a similar large species occurs in the Eifelian Imachinsk Suite of the Transbaikal region, USSR (Modzalevskaya, 1968).

The remaining published evidence concerns the conodonts. Philip (1966) and Philip and Jackson (1967) have argued strongly that the occurrence of such species

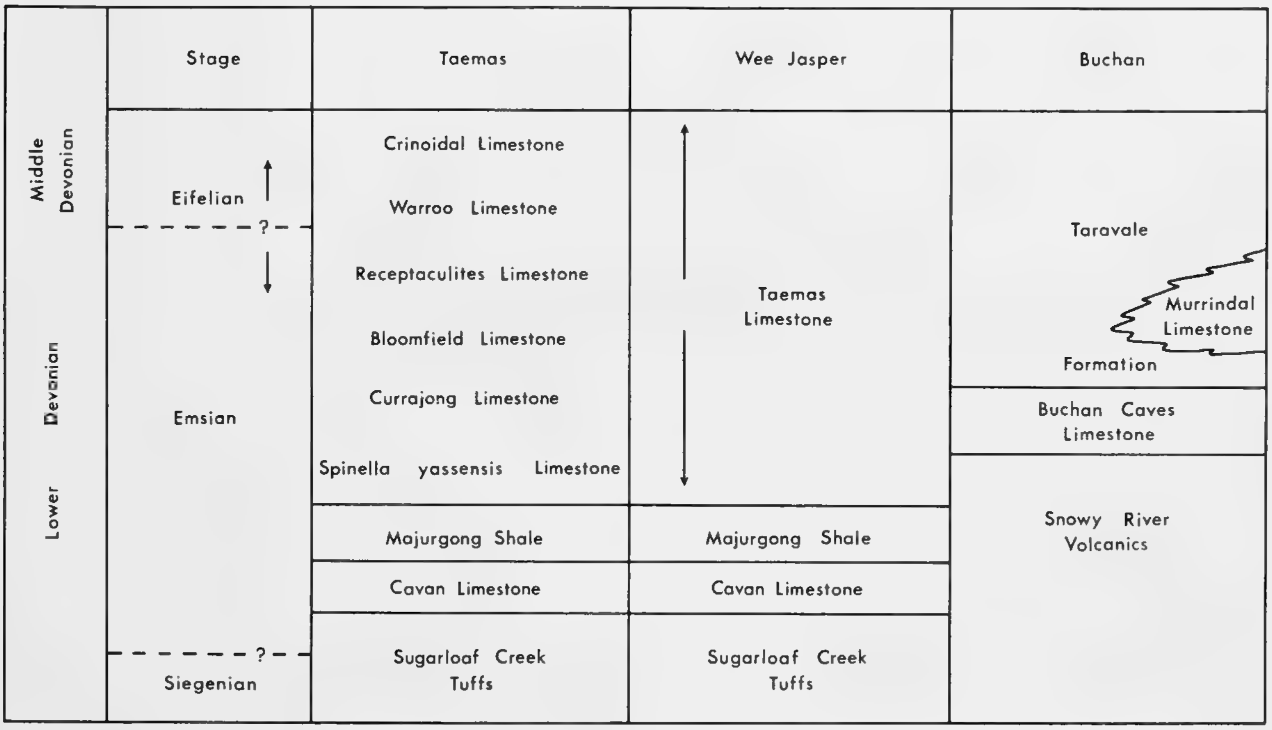


FIG. 1. Stratigraphical correlation of the geological sequences in which *Dipnorhynchus sussmilchi* and associated faunas have been found.

as *Ozarkodina typica denkmanni* Ziegler, *Plectospathodus alternatus* Walliser, *Spathognathodus inclinatus* (Rhodes) and *Trichonodella inconstans* Walliser, indicate that the *Xystriphyllum mitchelli* Fauna cannot be younger than late Emsian, and further that it is not latest Emsian. However, all of these species are generalized long-ranging types; it would be surprising if their terminal occurrences were contemporaneous the world over. More significant is the occurrence of *Polygnathus linguiformis foveolatus* Philip and Jackson with *P. linguiformis linguiformis* in the top of the fauna apparently without the distinctive Eifelian species of *Polygnathus.* The absence of icriodids hinders solution of this problem.

The conclusion we reach from data at present available (Fig. 1) is that *Dipnorhynchus sussmilchi* occurs in rocks no older than early Emsian and no younger than early Eifelian. Further work on ostracods, tentaculitids, and such brachiopod groups as the rhynchonelloids is needed to reach more precise conclusions.

THE SKULL ROOF OF PALEOZOIC DIPNOI

DEFINITION OF THE DERMAL BONES

In large part, as will be seen in later discussion, interpretation of the phylogeny of Dipnoi depends upon a detailed investigation of the homology of the dermal bones of the skull roof. It is well known (e. g., Westoll, 1949; White, 1966) that the dermal-roofing pattern of Dipnoi is different from that of other groups of fishes, but is fully consistent within the Dipnoi. Forster-Cooper (1937), Romer (1936), Westoll (1949), and White (1965) have been the principal contributors to our understanding of the homology of the dipnoan skull roof, which has developed with the aid of the elegant system of notation developed by Forster-Cooper. The fact that *Dipnorhynchus* shows a more complicated (and presumably more primitive) skull roof pattern than that of *Dipterus*—the genus upon which previous studies have been based—has caused us to re-evaluate the general situation concerning dermal bone patterns in Dipnoi. A first step in such a task is the development of a comprehensive set of definitions for the dermal elements. In preparing such definitions there are several requirements that must be met.

1) A means of tackling the problems of fusion, or invasion, or both must be provided. We have accepted Parrington's view (1949, 1956, 1967; see also White, 1966) that fusion of bones should not be postulated on topographic evidence alone. There seem to be only two other independent lines of approach to the recognition of fused elements. The first of these is the presence of more than one center of ossification, a phenomenon that is only rarely observed. The second concerns only bones on which two lateral-line canals, or a lateral-line canal and a pit line, join. It is best illustrated by reference to the K and X bones of *Dipterus* and *Scaumenacia*. The normal situation in *Dipterus* is represented in Fig. 2A. In Fig. 2B the shape of the bone suggests fusion; this is confirmed by the relative positions of the lateral-line canals. Ossification must have been initiated at both canal junctions. The canals in *Scaumenacia* shown in Fig. 2C indicate a single center of ossification and thus illustrate the capture of the canal issuing from "J" by bone "X," which is not compound. Bone "K" has been eliminated.

Where neither of these situations can be established, we have assumed space capture by one of the adjacent bones: which bone it is not always possible to determine. Some of the problems are outlined subsequently.

2) Criteria for the recognition of homologous structures must be agreed upon. Most work in the field is based upon topographical interrelationships and relations to lateral-line canals and pit lines (for summary see Westoll, 1949; Parrington,

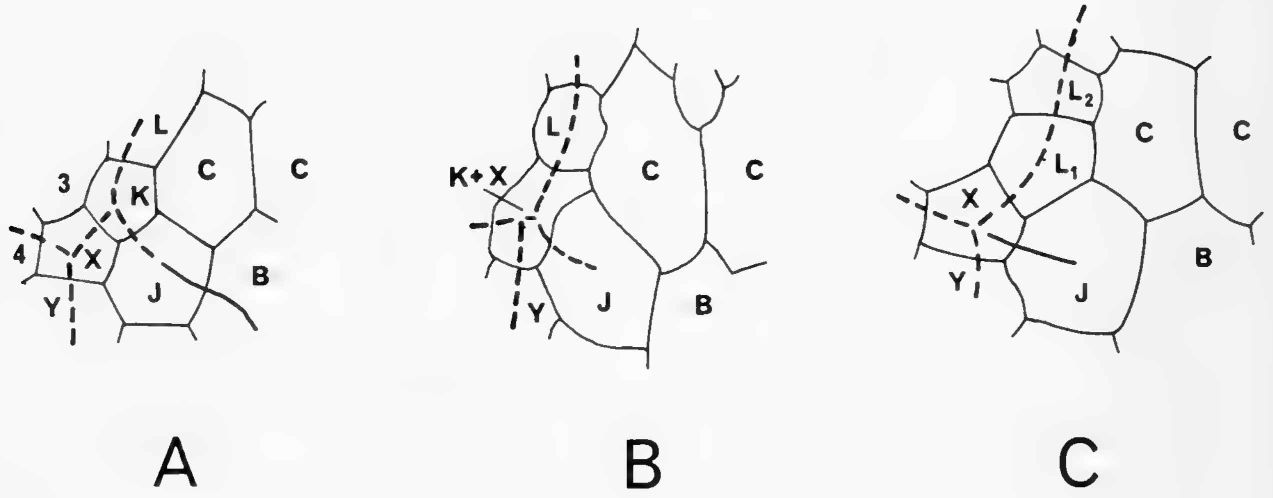


FIG. 2. Portion of the left side of the skull roof in three specimens of Devonian Dipnoi, showing variation in dermal bone pattern. A) *Dipterus valenciennesi*, "normal situation," specimen 33165, British Museum (Natural History); B) *Dipterus valenciennesi*, specimen showing possible fusion of X and K and subsequent modification of the lateral-line canal pattern, specimen 33165, British Museum (Natural History); C) *Scaumenacia curta*, "normal condition" showing that in this case bone K has been eliminated, specimen E 2853, Park Museum. Redrawn from Westoll (1949) and White (1965).

1956 and 1967). We would like to re-emphasize the importance of relation to the structures of the chondrocranium, particularly in the identification of the posterior roofing bones.

3) A standard for the comparison of dermal bone patterns must be established. In the past the skull roof of *Dipterus* has been used as a standard, following the work of Forster-Cooper (1937). However, *Dipnorhynchus sussmilchi* (and also *Uranolophus)* presents a more complex pattern that is both geologically and phylogenetically more primitive. Bones unknown in *Dipterus* now have to be named. Moreover, since the Forster-Cooper system of notation can be adapted to *Dipnorhynchus* with only minor modifications, and since a comparative study of *Dipnorhynchus* helps clear up certain problems in the interpretation of *Dipterus* itself and other forms (see below), we choose *Dipnorhynchus* as a new basis for comparison.

4) An integrated sequential system of analysis should replace the current *ad hoc* approach to the identification of bones. That is, using a given bone as a primary reference point, other bones should be defined in sequence; each definition must be cast only in terms of entities defined earlier in the sequence.

5) The initial reference bone must be one that can be readily recognized in all genera, is not the subject of argument about fusion or splitting, and provides a starting point for a sequence that will extend to all or most of the other bones. Bone "B" satisfies these requirements best.

6) A knowledge of the phylogeny of the group is desirable but is not yet available. On the other hand, the stratigraphic succession of genera is known, and this information is adequate for present purposes.

The definitions that follow (see also Fig. 3) aim at satisfying these requirements. When qualification is necessary, it is clearly indicated.

Bone "B" is the median bone lying over the posterior part of the braincase, anterior to the occipital commissure of the lateral-line canal, and either carrying the ends of the anterior pit lines or lying between them.

Bone "I" can then be defined as an element carrying the posterior pit line, in contact with the posterolateral margin of B, and supported on its ventral surface by the dorsolateral crista of the braincase.

"A" is a median bone carrying the occipital commissure, in contact with "I" on its anterolateral edges, and usually also in contact with "B." It lies behind the median crista of the braincase and is loosely attached along its anterior and lateral edges.

Bones "C" are paired bones immediately anterior to "B." They may be fused medially as an individual variation *(Dipnorhynchus)*.

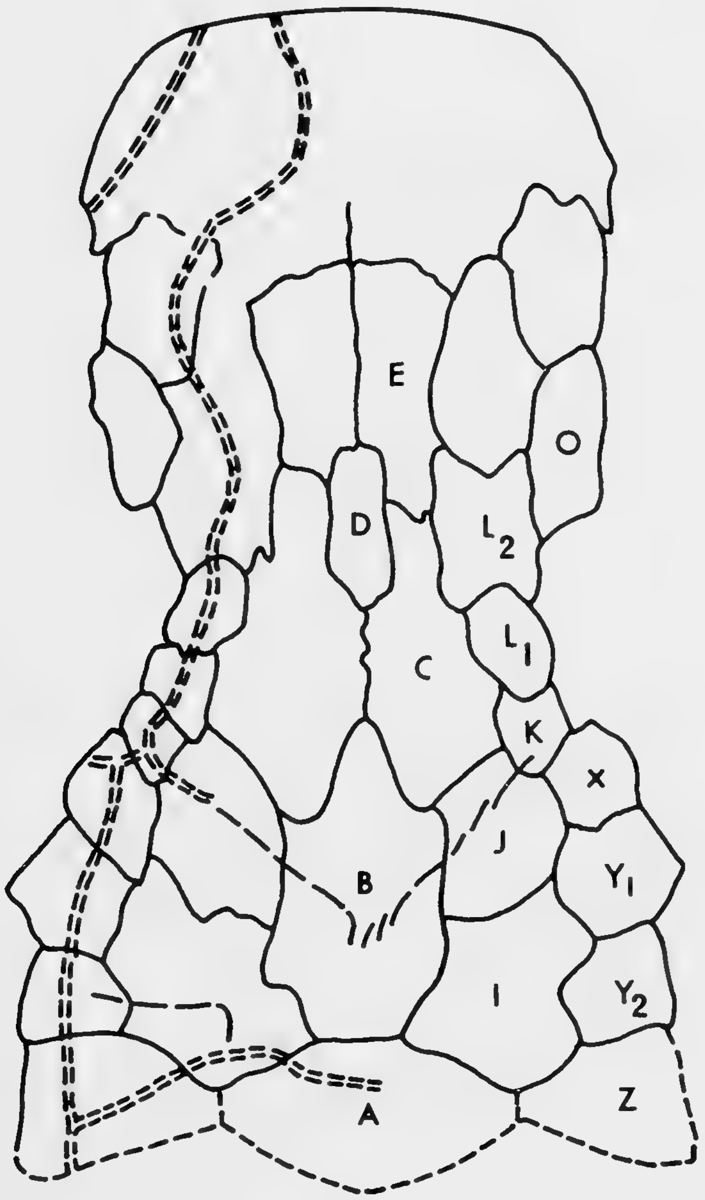


FIG. 3. *Dipterus valenciennesi,* skull roof showing "normal" arrangement of dermal bones and lateral-line system. Redrawn from White (1965) with bones labelled according to the system developed here. Specimen P 7834, British Museum (Natural History).

In the bone series anterior to "C" there are at present no clearly defined reference points that enable homologies to be decided. The position of the pineal foramen, or where that is not present the pineal stalk, offers a possible solution to part of the difficulty, but the problems involved are great. They are later discussed under *Soederberghia.*

Bone "J" lies immediately in front of "I" and lateral to "B," carries the anterior pit line and, in the more primitive genera, the posterior end of the supraorbital lateral-line canal from which the anterior pit line evolved.

Bone "X" has a contact with the anterolateral or the lateral edge of "J" and contains the junction between the main and the infraorbital lateral-line canals.

Posterior to "X" is the lateral-line bone "Y," often divided into two elements "Y_1" and "Y_2." It is flanked laterally by the operculum. Where "Y_1" and "Y_2" are present, either one contains the lateral extremity of the posterior pit line; the ventral surface of either or both makes contact with the palatoquadrate. Where one "Y" only is present, both these structures can be observed on the posterior half of the bone. It seems impossible to decide in many circumstances if "Y_1" has captured "Y_2" or vice versa. Hence when one bone only is present it is usually simply labelled "Y."

Bone "Z" forms the posterolateral corner of the skull, is loosely articulated, and contains the junction between the main lateral-line canal and the occipital commissure.

Bone "4" (occasionally divided into "4a" and "4b" as in *Soederberghia)* is usually circumorbital, but may be excluded from the orbit as an individual variation (as in certain specimens of *Dipterus valenciennesi).* It is the most dorsally placed element on the infraorbital canal below the element on which the junction between the infraorbital and supraorbital canals takes place. As indicated above this is almost invariably bone "X.'

Bone "3" lies anterior to "4" and forms the upper rim of the orbit. Bones "2" and "1" follow "3" around the orbit, "1" forming its anterior margin.

Bone "O" (sometimes divided) is a nonlateral-line bone lying between "3" and "2" on the outer side and the lateral-line bones on the inner.

Bone "K" lies anteromedial to "X" and lateral to "C." It also carries the supraorbital canal that runs forward from "J."

Bone "L" (sometimes divided) is on the supraorbital lateral-line canal medial to "3" and "O," or medial to "3" and "2" where "O" is not developed. Its posterior edge is in contact with "K," or with "X" when "K" is not developed.

The supraorbital lateral-line bones "M," "N," "P," etc. anterior to "L" vary in number, shape, and position depending on the shape of the snout; it is difficult, if not impossible, to offer definitions of them that are generally applicable. Where "O" is present "M," "N," and "P" can be defined as having contact with it, but even then it is not possible to differentiate between them severally with certainty.

The bones of the cheek are known in detail in only three Paleozoic genera—*Dipterus, Fleurantia,* and *Soederberghia*—in all of which the distance between the orbit and the operculum is much smaller than that between the orbit and the snout. The circumorbital bone "5" (Fig. 4), which is placed below "4," contains the junction between the preopercular (or jugal) and infraorbital lateral-line canals. Bone "8" lies posterior to "5," receives the jugal canal from it, and passes it to bone "9" which forms the posteroventral angle of the cheek. Bones "4," "8" and "9" are in contact with the operculum posteriorly. The infraorbital canal traverses bones "5," "6," "7," and "1" in sequence around the ventral half of the orbit, the latter three bones also forming part of the ventral edge of the skull. The identification of bone "1" is sometimes conjectural.

In addition to the bones defined above there are two others—"T," known in *Dipnorhynchus,* and "H," inferred in *Dipnorhynchus* and *Uranolophus.* It is not proposed to define them until *Dipnorhynchus* is discussed in detail. Full definitions will be found on p. 28.

In a group in which variation is so marked as the Paleozoic dipnoans, it would be naive to suggest that the above definitions will prove applicable in every instance. In particular, the topographic relationships of bones are likely to vary, even within a species, to such an extent that they cannot be recognized by their position alone. However, bones subject to such variations can usually be recognized either by the nontopographical criteria in the definitions, by comparison with normal specimens, or by a process of elimination. Examples are readily to hand in the work of White (1965, fig. 21) on *Dipterus valenciennesi,* one of which is presented in detail here as an illustration (Fig. 4). In this specimen, bones "A," "B," "C," "I," "J," "Z," "5," "8," "4," "3," "2," and "O" can all be recognized by application of these definitions in their entirety. This leaves only the bones White labelled "Y_1," "K," and "L_1," to be accounted for. There is clearly one bone less in this series than in the same position on the standard and most other specimens. The problem is to decide the fate of this bone. The bone labelled "K" satisfies the topographical relationships given in the definition of "K" with respect to "3" and "J," and it receives a lateral-line canal from "J." Apart from the fact that it does not join a normal "X" on its posterior margin it has no peculiarities and is therefore probably correctly identified. The bone labelled "Y_1" then fails to satisfy the definition in that it is

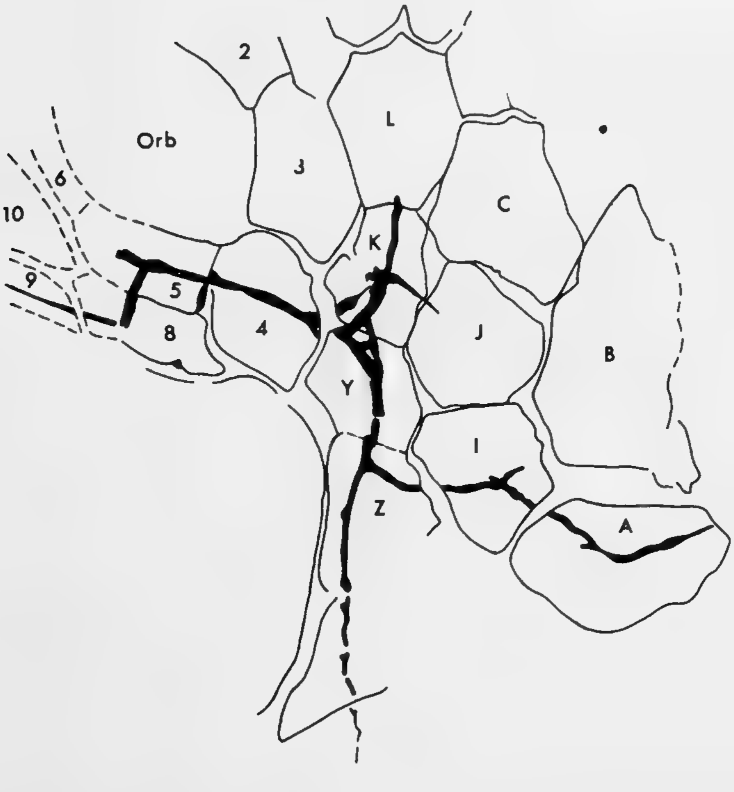


FIG. 4. *Dipterus valenciennesi.* Posterior skull roof and cheek elements, showing lateral-line canals. Redrawn after White (1965) with additional original observations.

bounded in front by "K" rather than "X," it contains the junction of the infraorbital and supraorbital canals, and it adjoins "4." The two latter features are usually characteristic of "X." On the other hand it lies on the lateral-line canal anterior to "X" and is flanked by the operculum and by "I_2," as is normal for a "Y" bone. There are thus three possibilities. The bone White labelled "Y_1" is: 1) an abnormal "X" and "Y" is not present; 2) a fused "X" and "Y;" or 3) an abnormal "Y," and "X" is not present.

There are no signs of two centers of ossification on the bone in question, but it does contain the junction of the infraorbital and main lateral-line canals, a feature associated with "X." It is unlikely to be an abnormal "X" however, for not only would it flank the operculum, but it would also be the only bone available to contact the palatoquadrate. Both of these are characters of "Y" bones. Moreover, the tendency of the canals to focus in a most unusual way on the point of junction of "4," "K," and "Y" suggests an accommodation to the failure of a bone to develop in that position. Such a bone could only be "X." The most reasonable solution therefore is (3), above.

THE SKULL ROOF OF *DIPNORHYNCHUS SUSSMILCHI*

Previous Work

The first major attempt at an analysis of the skull roof of *Dipnorhynchus sussmilchi* was that of Hills (1941). Prior to this, Etheridge (1906) and Hills (1933) had described the external character and arrangement of the bones, but since nothing was known of the lateral-line system the homologies could not be soundly based. The analysis of Hills (1941) has been taken as definitive by all subsequent workers; so far as we are aware no reexamination of the species was attempted until that of Campbell (1965), which was based on a new specimen. The latter involved no reinterpretation of the roof; and the bone nomenclature of Westoll (1949) was used pending more adequate preparation of the specimen. Denison (1968a) has recently reinterpreted the dermal bone homologies of the species on the basis of this latter description and casts of the specimen supplied by us.

In his restoration of 1941 Hills made two major errors—concerning the arrangement of the bones on the occipital region of the skull and the position of the orbit. The posterior part of the roof of the type specimen was not preserved; so he reconstructed it in the light of the known structure of other Devonian dipnoans, particularly *Dipterus* and *Fleurantia*. Unfortunately, this part of *Dipnorhynchus* shows little resemblance to these other genera, as was shown by the discovery of another species, *D. lehmanni* Westoll, in Germany (Westoll, 1949), in which the "lateral extrascapular 1" of Hills was shown to be very much larger than he had suspected.

The occipital commissure of the lateral-line system was not preserved on either *D. sussmilchi* or *D. lehmanni,* but both Hills and Westoll indicated that it passed through the "lateral extrascapular 1" (i.e., bone "I" of Westoll). Our new material shows that the canal does not pass through this bone. Presumably it lay in the bone behind, but this is not preserved. Previous attempts to identify the bones in this region of the skull were therefore doomed to failure.

The second error, which has had more far-reaching effects, developed from a misunderstanding of the relationship of the infraorbital and main lateral-line canals. The canal that Hills interpreted as the infraorbital was not completely excavated; on further preparation it has been found to be a shorter anterior offshoot that does not extend forward onto any other element. In fact the infraorbital canal makes a lateral bend in the bone behind the one containing this anterior offshoot (bone X in Figure 5B) and passes down into the cheek bones. This mistake can be readily understood, for in *Dipterus* the infraorbital canal is given off in the most anterior bone penetrated by the main canal. The incorrect anterior position of the orbits inferred from this information has meant that most bone homologies have been misconceived. This has not been recognized by Denison (1968a, p. 361) who believed that Hills correctly identified "X." The apparently obvious "B" and "C" bones, for example, were interpreted as "B_1" and "B_2" by Westoll (1949) because they were so far back relative to the orbits; and for similar reasons White (1965, p. 26–31) has been led into a new but, we believe, erroneous theory of the early evolution of the rear end of the dipnoan skull.

NEW DATA.

The homologies of the roofing bones of *Dipnorhyncus sussmilchi* will now be discussed using the principles previously enunciated (Figs. 5 and 6). The two avail-

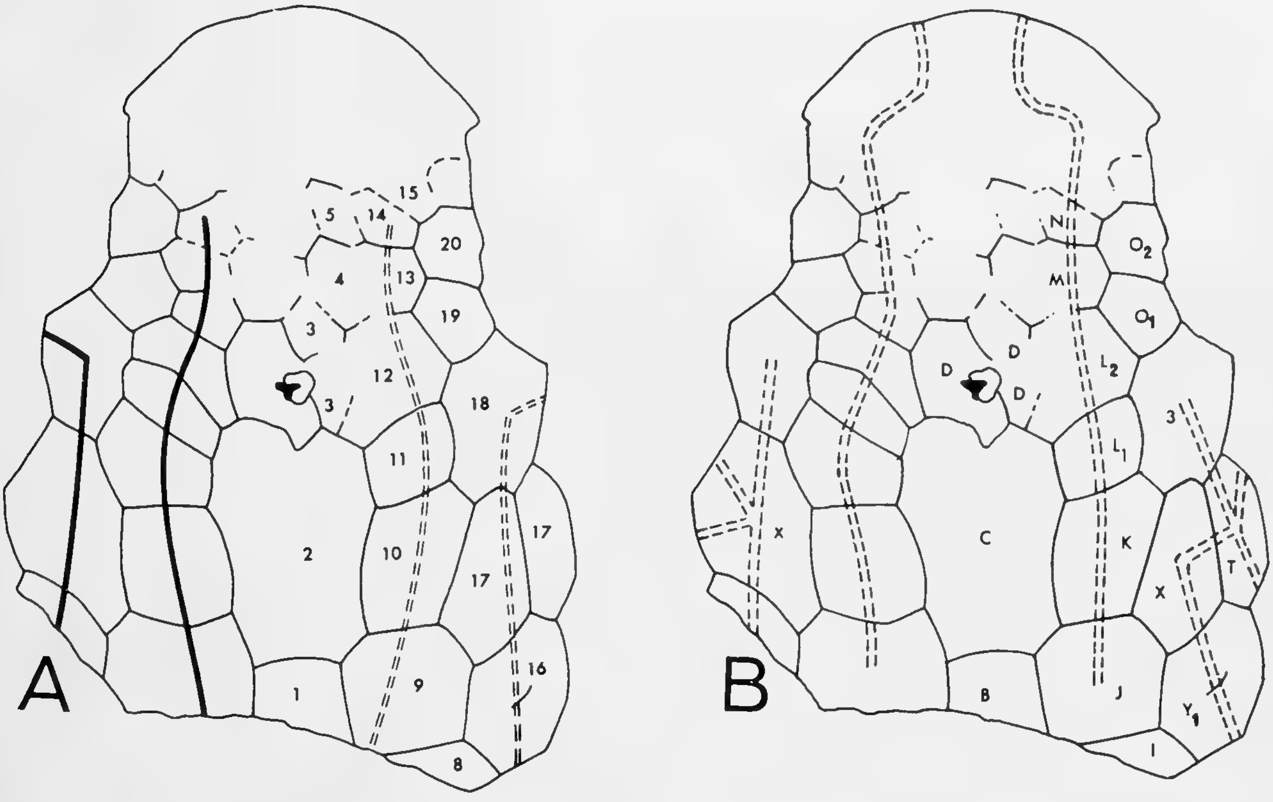


FIG. 5. *Dipnorhynchus sussmilchi,* Holotype. A) Hills' drawing of the skull roof, original notation. B) new reconstruction of the skull roof with new notations. Redrawn from Hills (1941) and original.

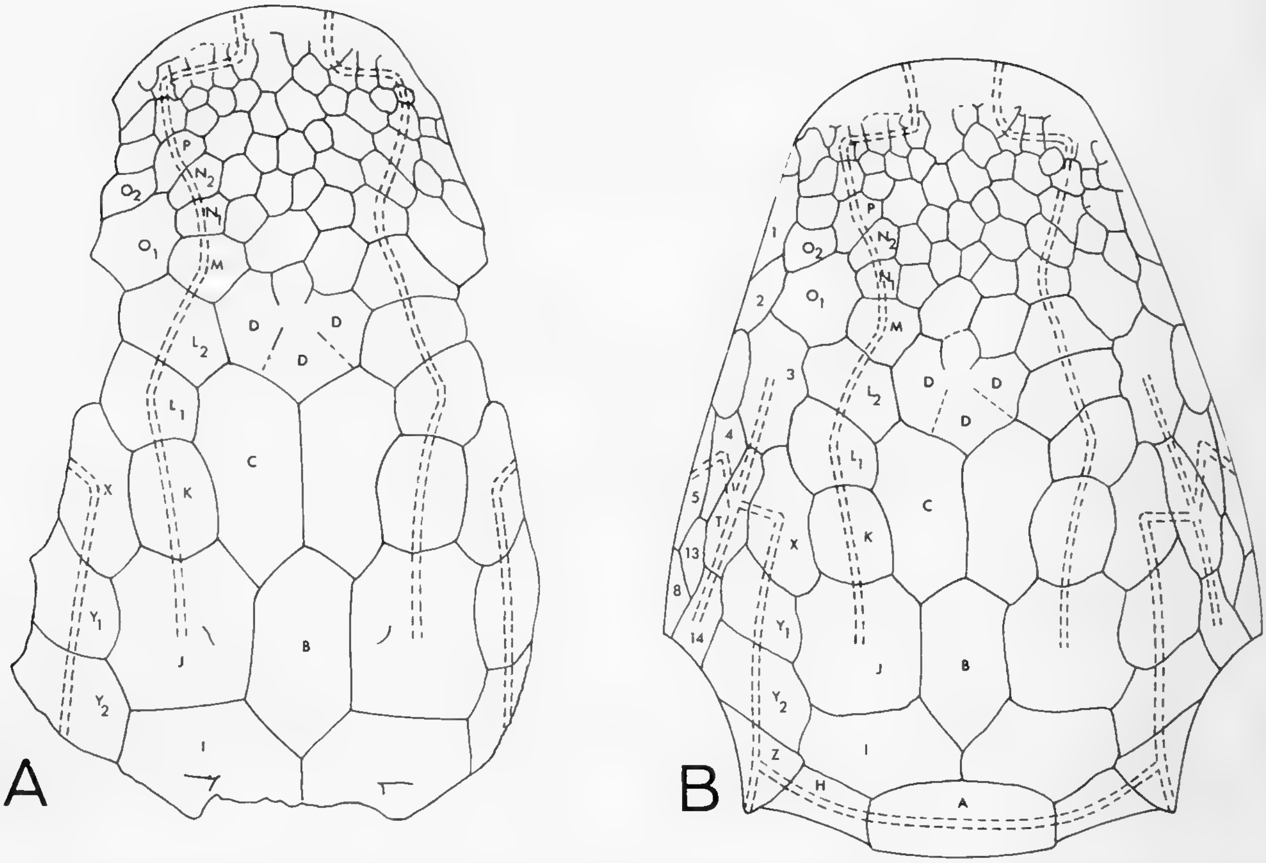


FIG. 6. *Dipnorhynchus sussmilchi,* Specimen 18815. A) drawing of the skull roof. B) reconstruction of the skull in dorsal aspect. After Campbell (1965) and original.

able specimens are different in several features; this necessitates a separate discussion of the bones seriatim.

Bone B and the paired bones C can be readily recognized using the standard definitions, though in one specimen the pairing of the C bones is only incipient.

The bones lying posterolaterally to B and joining along a median suture behind it carry short posterior pit lines that divide at their inner extremities, but do not extend laterally. However, they do *not* carry any part of the occipital commissure of the lateral-line system. On their ventral surfaces they support the dorsolateral cristae that enclose the anterior vertical semicircular canals (see "Braincase"). They satisfy the definition of "I" but are decidedly unusual in their transverse shape and the absence of the occipital commissure. At this juncture they will be tentatively identified as I.

As has been indicated previously (Campbell, 1965) there is a median embayment in the posterior edges of the I bones of specimen 18815. On preparation this excavation was found to have a "stepped" edge that was almost certainly an articulatory surface for a loosely attached bone "A." It is possible to restore this bone approximately from the shape of the contact, as shown on Figure 6B. There is no sign in the newly prepared material of a lateral-line canal passing out of the posterior edge of the I bone; since A normally carries the occipital commissure of the lateral-line canal, it must be concluded that this commissure passed entirely posterior to the fixed I bone. The posterior edge of the skull roof lateral to the contact with A in specimen 18815 is almost completely preserved and shows a sharp cosmine edge surmounting a grooved surface on the bony layer. It is quite dissimilar to the flat, transversely striated sutural surfaces of a fixed roof bone. On the contrary it suggests the presence of loosely articulated bones along its entire length. One of these would be "Z," the bone that in *Dipterus, Fleurantia, Scaumenacia,* and *Sagenodus* carries the junction between the main lateral-line canal and the occipital commissure. Bone Z is small and subtriangular in all these genera, except *Dipterus* in which it is very transverse and in contact with A along its medial edge. As has been already demonstrated, A in *Dipnorhynchus* is relatively small, and if Z were the only element between A and the operculum, it would be an enormous transverse bone, larger than any other in the skull roof. It is unlikely that a loosely articulated bone with such a shape could have existed in this position, since the articulatory edge is arched and movement along an arc of the length postulated would be difficult. It is more likely that there was a smaller lateral Z and another small bone between it and A. This additional bone would be the posterior continuation of the "I" series, and would in fact be the element designated "I_1" that has been postulated in the ancestor of *Dipterus* and observed in *Rhinodipterus secans* by White (for summary see White, 1965, p. 23–26). Having used "I_1" in this way, White designated the fixed "I" bone as "I_2." However, since there is no suggestion that "I_1" and "I_2" ever fuse to form a single "I" element, it would seem to be more reasonable to retain the index "I" for the fixed bone and use "H" for the unattached bone behind it. The symbol "H" is available and is a logical choice, since White used "Z" for the small triangular bone posterior to "Y." Denison (1968a, p. 357–358) has already used it in this sense. Bone "H" would then be defined as an element lying between "Z" and "A" and carrying the occipital commissure of the lateral-line canal. H, A, and Z are not to be considered as forming part of the skull roof proper. Strictly speaking, they are extrascapular elements.

On both specimens "J" is recognized by the standard characters—position with respect to "B" and "I" and the presence of the anterior pit line. It also contains the termination of the supraorbital lateral-line canal as does its homologue in *Dipterus.* It should be noted, however, that the pit line is situated further back on the bone than in other genera, and that it is directed toward a point well behind the midpoint of "B."

The position of the junction of the infraorbital canal with the main lateral-line canal can be determined on each side of both specimens of *D. sussmilchi,* not only from the external pores, but also from the positions of emergence of the canals on the bone margins and from X-ray photographs. It is also quite clear that there is no connection between the main lateral-line canal and the supraorbital canal as there is in *Dipterus.* The arrangement of the canals is shown in Figure 6B. The bone in which the infraorbital and main lateral-line canals meet is large and equidimensional on the left side of the specimen F 10813A. The same space on the right side is occupied by two bones and it is clear that two bones were present in the same position on both sides of specimen 18815, even though on neither side is the outer bone preserved. It is apparent therefore that the left side of specimen F 10813A is atypical, a most unfortunate fact since it was on this side that Hills prepared the lateral-line canals.

In discussing the homologies of the bones in this region, let us begin with the application of the standard definition and assume that, on the three normal sides, the bone in which the infraorbital and main canals join is "X." The infraorbital canal passes out of these bones laterally into a similarly shaped bone where it branches into three. One short branch passes forward into "3," a second downward into what must be another (unpreserved) circumorbital, and a third backward into a cheek bone (unpreserved) lying below "Y_1." What is the identity of this bone where the trifurcation takes place? The only preserved example of it is entirely bordered by sutures; hence it is not a normal "4," though occasional specimens of *Dipterus* in which "4" is excluded from the orbital margin are known (Westoll, 1949, figs. 2F, 3G, 3I). Moreover no other genus is known in which "4" contains a branching canal system of this type. On the other hand, if it is not a "4" it can only be a supernumerary element not known in any other genus. To facilitate discussion let us provisionally label it "T." This would mean that the element lying anteroventral to T must be the circumorbital "4." Support for this view comes from the angle at which the infraorbital canal emerges from "T." The shape of the orbit can be reconstructed from the part of its edge preserved on "3;" the center of radiation of the bone that filled the space between "T" and the orbit can be determined approximately from the angle at which the infraorbital canal enters it. As can be seen from Figure 7A, this bone must have been relatively small and shaped somewhat as shown. Such a bone could not be "5" (as it would have to be if the element labelled "T" were in fact "4"). If it were "5," the cheek bone "8" (see below) would have to fit in the angle between "Y_2," "T," and "5" in order to receive the preopercular canal. It would then also have to receive the canal that runs posterior from "T;" it is clear from X-ray study that it does not. Therefore, the only remaining possibility is that the circumorbital on the lower side of "3" must be "4."

A similar argument can be developed from the left side of the specimen where, despite the fact that the space occupied by "X" and "T" on the right is occupied by a single bone, the infraorbital canal emerges on approximately the same orientation, and the shape of "4" is comparable to that on the left.

Consequently we conclude that the bone labelled "T" on the right side of specimen F 10813A is not the homologue of any bone in *Dipterus,* and we retain the designation "T" for it. On the left side of the same specimen, since there is no sign of two centers of radiation, the single bone in which the canals divide must be either an "X" that has captured the space and canals of "T" or *vice versa.* We can offer no convincing arguments for either possibility.

Posterior to "X," on both sides of specimen 18815 there are two large lateral-line bones. These must be a pair of "Y" elements and are designated "Y_1" and "Y_2" in the order proposed by White (1965, p. 12). No pit lines can be positively identified on them because they are extensively cracked, but there may be a short transverse one on the posterior element on the left side. "Y_2" and the posterior edge of "Y_1" meet the palatoquadrate on their ventral sides.

On the left side of specimen F 10813A only a fragment of the "Y" element posterior to "X" (or "T") remains, but on the right side almost the complete bone is preserved. From the Westoll-lines on this element and the adjacent fragment of "I," it can be demonstrated that there is a "Y_2" element also, though it is probably much smaller than the "Y_1." Unlike the palatoquadrate on specimen 18815, the one here is attached mainly to the posterior part of "Y_1" though it possibly extends back a short distance on the "Y_2." As was shown by Hills (1941, fig. 5), there is a well-defined, medially situated, oblique pit line on "Y_1."

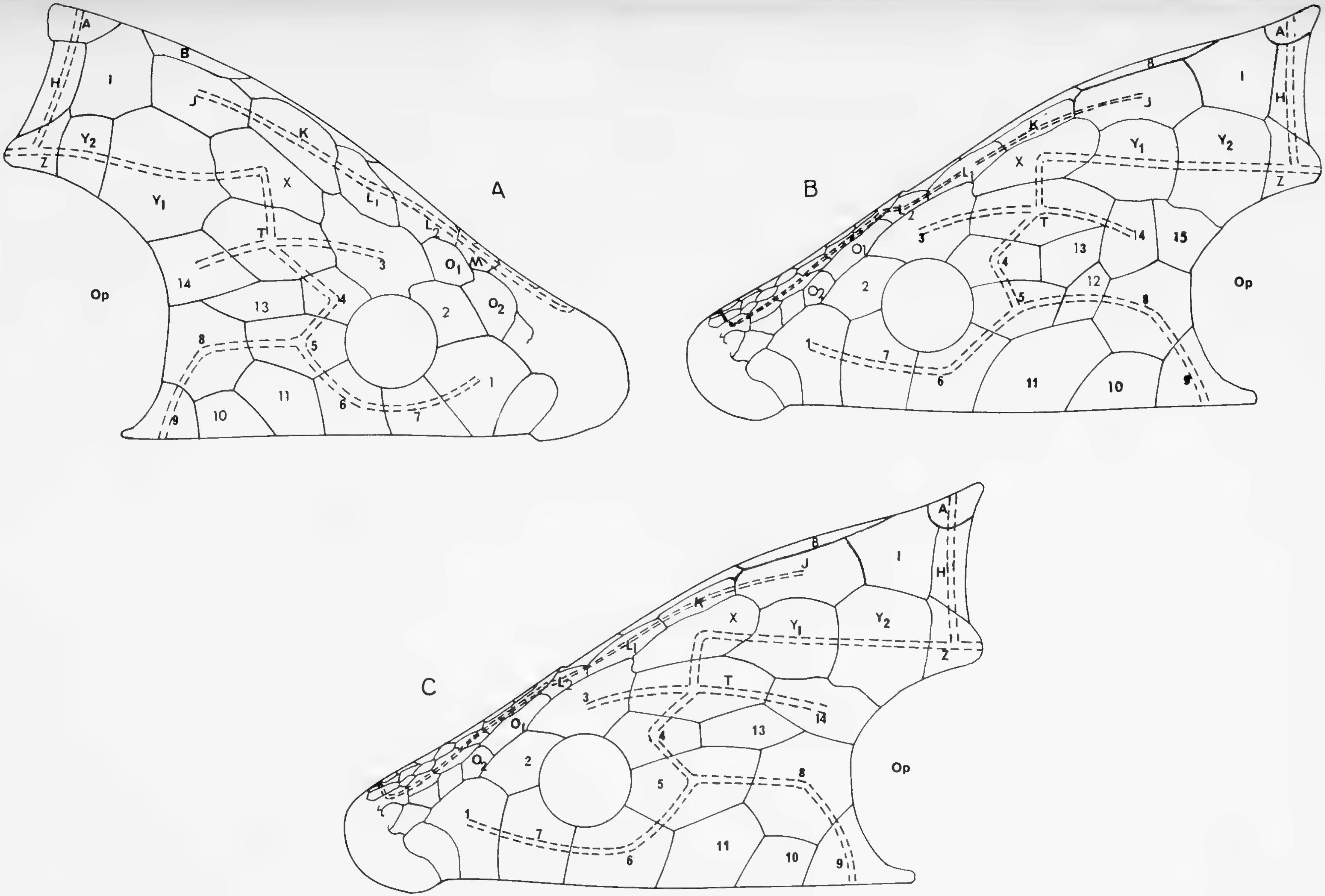


FIG. 7. *Dipnorhynchus sussmilchi*, reconstructions of the cheek. A) holotype, right cheek. B) and C) specimen 18815, alternative reconstructions of the left cheek. Note that in Figures 7B and 7C bone 1 is excluded from the orbit. Bones 6 and 7 could have been made smaller so that 1 could be fitted in at the orbital margin. Had this been done we would have had to insert another bone between 1 and the snout in order to keep its size within reasonable bounds. In the absence of any other evidence to support the presence of such a bone, we have preferred the present reconstructions.

The two specimens differ markedly in the way the "Y" elements are modified to accommodate the operculum. The posterolateral corner of "Y_1" on specimen F 10813A is beveled and presumably the whole lateral edge of the missing "Y_2" must be similar. On specimen 18815 the operculum could not have come so far forward, since only the posterolateral tip of "Y_2" and all of "Y_1" are normally sutured, and delineate the upper outlines of cheek bones.

Once the identity of these bones is established it becomes possible to solve the vexing problem of the homologies of the lateral-line series anterior to "J." In *Dipterus* the first of these bones is "K;" Denison (1968a) has identified it as such in *Dipnorhynchus.* However, in the latter genus it has several peculiar characteristics: it is not in contact with 3; it lies medially rather than anteromedially to "X;" and the distribution of sensory pores on "X" suggests that a cross-commissure of the lateral-line system could develop to the second bone in front of "J." These facts could be interpreted to mean that Denison's "K" in *Dipnorhynchus* is a supernumerary that is lost in all subsequent genera. However, any assessment must take account of the shortening of the cheek and the more posterior position of the orbit with respect to the braincase in *Dipterus.* This backward movement means that "3" and "4" are also further back; consequently "X," "Y_1," and "Y_2" are relatively shorter, and "X" moves back a little with respect to J. Consequently "K" would come to lie anteromedially to "X" and its outer edge would come into contact with "3." From an evolutionary point of view, Denison's identification of "K" is reasonable. The alternative view that his "K" is a supernumerary implies that his "L_1" is really "K." This cannot be substantiated since the bone in question lies in front of the midbrain whereas the standard "K" in *Dipterus* lies opposite it. We therefore support Denison's interpretation.

The homologies of all bones behind a line joining the middle of the orbits have now been established; those of the elements in front of this line present a much more difficult problem. There are two main reference features that can be used with confidence—the circumorbital bone "2," and the pineal stalk. Bone "2" is not preserved on either specimen, but its shape can be inferred with reasonable accuracy from the outline of the orbit on "3," and the sutures on the roofing bones in front of "3." In specimen F 10813A there are two approximately equal equidimensional bones between "2" and the lateral-line series; these are labelled "O_1" and "O_2." A similar pair occurs on the left side of specimen 18815, but on the right side the anterior one is longitudinally divided. The fact that these "O" bones are present is of importance, for "O" occurs in *Dipterus* but not in later genera. Moreover, there are, in both specimens of *D. sussmilchi,* two or three fixed bones anterior to "O_2" lying outside the lateral-line bones. These have no homologues in *Dipterus* in which this region is occupied by the large lateral-line bone "P." There is little point in formally naming them.

The lateral-line bones anterior to "K" are difficult to homologize in terms of the standard nomenclature for *Dipterus.* White (1965, p. 15) uses the convention that "P" in *Dipterus* is the bone where the lateral-line canal turns forward before swinging in toward the snout. There is no reason why this criterion should be applicable in other genera, or indeed why it should be consistent in *Dipterus.* Perhaps a better definition of "P" for that genus would be in terms of its position anterior to "O" and joining the circumorbital "1." As indicated previously, no lateral-line bones are in contact with "1" in *Dipnorhynchus,* but a pair of bones lying anterior and anterolateral to "O_2" and occupying the region of the lateral line just posterior to its medial swing, can be homologized with "P."

"L," "M," and "N" are in contact with "O" on their outer sides; "L" is also in contact with "K" and "C." By using these definitions the "L" bones can be easily identified in both specimens of *D. sussmilchi* except on the right side of specimen 18815 where "L_2" just fails to make contact with "O_1" because of the peculiar shape of the bone in front. Its identity, however, is not in doubt. "M" and "N" are so variable in *Dipterus* and show such a wide range of shapes and invasions that no satisfactory definitions can be developed for them. In *D. sussmilchi* the bones thus named seem to occupy areas comparable with corresponding bones in *Dipterus.*

The lateral-line bones anterior to "P" number four or five on each side of specimen 18815 and probably at least three on each side of specimen F 10813A. They have no homologues in *Dipterus* and are not named here.

The "D" bones of *Dipterus* also show a dismaying variability. If the type skull only is considered, and lip service is paid to the probable, but unproven, hypothesis of the fusion origin of "D," it is reasonable to label the bones grouped round the pineal foramen in *Dipnorhynchus* as "D."

There is no point in attempting to group the median bones anterior to "D" into any scheme. It should be noted, however, that enough of the outlines can be distinguished beneath the cosmine of specimen F 10813A to conclude that there are fewer and larger bones in this region than in specimen 18815.

THE CHEEK OF *DIPNORHYNCHUS SUSSMILCHI*

No cheekbones have been found associated with either of the skull roofs, but in the vacuity of the mandible from Buchan a large lateral-line bone was found to be lodged that we believe is from the cheek of the same specimen. This bone is approximately an equidimensional polygon in shape and is bounded by sutural margins on all sides except one, along which it is beveled. It is traversed by an unbranched angular lateral-line canal the course of which can be traced by X rays and checked from the points of emergence. An array of fine tubules is given off from the main canal on either side of the median angular flexure (Fig. 91B; Fig. 95). A short submedian, arcuate pit line is present. The thickness is uniform except along half the beveled edge and the adjacent edge that contains an end of the lateral-line canals. Toward these two edges the bone is distinctly thicker.

We consider that it can only represent a cheek element, but the alternative possibilities must be briefly considered. Because of the beveled edge on this bone, which indicates a nonsutural margin, the number of possible positions it could occupy is limited to three—that of a "Y" element from the skull roof, a circumorbital, or a posterior cheekbone adjoining the operculum. If it were a "Y," then its orientation could be fixed by the position of the lateral-line canal. When this is done the beveled edge is too far forward for the right side of the skull and too far backward for the left. Further, the inner surface of the bone should show marks of the attachment of the quadrate ramus; though this bone is very well preserved there are no signs of such attachment. If it is a circumorbital, it has to be "4," "5," or possibly "6" since these are the only bones likely to have completely sutured edges apart from the one against the orbit. Of these, "6" can be eliminated because the course of the lateral line would be down rather than along the bone; in any case it has too many sutural boundaries. Bone "5" in *Dipterus* and *Fleurantia,* the only two Paleozoic genera in which it is known, bears the junction between the infraorbital and the preopercular (jugal) canals, but it has no pit line. On both these counts our bone cannot be identified with "5." Finally, "4" can be eliminated because, with the orbit and the suture with "3" fixed by the position of the beveled edge, and the junction with "X" fixed by the lateral-line canal, it can be seen that it could fit only on the left side, and then only if there were a roofing bone between "3" and "X," which is not the case. Also the presence of the pit line argues against its being a "4."

This leaves the hypothesis that it is a posterior cheekbone. If it is one of these, the lateral-line canal in it must be part of the preopercular (jugal) canal, and its orientation is appropriate if it comes from the right cheek. The presence of the pit line on it suggests that it is the homologue of bone "8" of *Dipterus.*

By assuming that the isolated bone "8" belonged to the individual with whose lower jaw it was found, it is possible to scale it down to the size of the available skulls and then fit it into the cheek. The overall dimensions of the cheek can be readily determined since the opercular edge on the Y elements and the opercular articulation on the palatoquadrate fix its posterior, the orbit its anterior, and the palate its ventral limits. It is obvious from these data (Fig. 7) that the cheek of specimen 18815 is proportionally longer than that of specimen F 10813, and that both of them are proportionately very much longer than those of *Dipterus* and later Paleozoic genera.

The difference in the relative sizes of the two cheeks shows that this region must have been variable; therefore bone outlines are unlikely to be stable, and it is possible that the larger cheek may have contained more bones. In these circumstances the outline of bone "8" cannot be regarded as being of vital significance, and alternative reconstructions are possible. Despite this, certain conclusions applicable to both specimens can be reached (Fig. 7):

1) Bone "8" contains no lateral line that could have originated in "T;" therefore there must be one or more bones between them. If it is assumed that "8" is normally heptagonal, there must be at least two. Of these, the element lying in the angle between "Y_1," "T," and "8" will be the one to receive the canal as can be seen from the direction in which the canal emerges from "T." We here designate this element "14." The nonlateral-line bone between "14," "T," "4" and "5" is designated "13."

2) The position and approximate shape of "5" can be fixed from the positions of "4" and the orbit, and from the fact that it must contain the junction between infraorbital and the preopercular canals.

3) At least in the specimen from which our "8" came, there must have been two bones ventral to it because of its shape and sutural characters. The posterior one would have been the homologue of "9" in *Dipterus,* since it would have carried the extension of the preopercular canal. This relatively small bone would be articulated with the palatoquadrate just above the jaw articulation and would therefore be somewhat thickened. This is in agreement with the thickening of our example of "8" in the corresponding direction. Presumably the anterior one would have been the homologue of "10."

Given these conclusions it becomes possible to discuss differences between the two specimens. In specimen F 10813, the inferred sizes of bones "8" and "5" suggest that they are in contact. If this is so, there is likely to be another bone ventral to both of them and anterior to "10." This could appropriately be designated "11" (see Fig. 7A). The shape of this bone, and of "6" and "7" that lie anterior to it, are entirely conjectural. However, there is good control on the shapes of "2" and "1."

On specimen 18815, the outline of the lower edges of "Y_1" and "Y_2" indicate the slight possibility of the presence of a bone between "14" and the operculum. This we have designated "15" in Figure 7B. Also it is conceivable that "5" and "8" were not in contact, and that there was a small lateral-line-bearing bone "12" between them (see Fig. 7B). The alternative reconstruction shown in Figure 7C is, however, considered to be the more probable.

THE CRANIAL LATERAL–LINE SYSTEM IN *DIPNORHYNCHUS SUSSMILCHI*

Many details of this system have been described in the previous section. It remains only to summarize the most distinctive of these and to complete the description (Figs. 6 and 7). The following features are noteworthy.

1) The occipital commissure must lie wholly on the loosely articulated bones Z-H-A-H-Z.

2) The trifurcation of the canal in T with canals running forward to 3 and backward to 14 is not known on any other dipnoan. However, as noted below, in *Scaumenacia* (Jarvik, 1968) there is a short canal onto 3.

3) As has long been known, there is no connection between the supra- and the infraorbital canals; the supraorbital canal extends backward from K to J. These two features are also known from *Uranolophus.*

4) There is no rostral commissure across the dorsal surface of the snout.

5) No junction of the supraorbital canals around the anterior edge of the snout has been demonstrated, though 18815 does show an almost continuous series of large pores around this region.

6) The position of the infraorbital canal has not been observed, but it can be inferred from the data given in the previous section. However, the large pores around the ventral edge of the snout figured by Campbell (1965, pl. 91) and apparently interpreted by Hills (1941, p. 49) as indicating the course of the infraorbital canal, are not connected with a lateral-line canal at all. They, together with the pores mentioned under (5), open into a ramifying set of tubuli occupying the space between the external dermal bones above and the dorsal and anterior wall of the nasal capsule below (see Figs. 69, 71). They are here termed *rostral tubuli.* In addition to opening to the external surface, these tubuli open through one large and numerous small foramina into the nasal capsule. Details of their structure and function are given below. A similar set of *rostral tubuli* occurs in the symphysial region of the lower jaw (see below).

COMPARISON OF *DIPNORHYNCHUS SUSSMILCHI* AND OTHER DIPNOI

Dipnorhynchus lehmanni Westoll. This is the only species, apart from the type, yet assigned to *Dipnorhynchus*. Lehmann and Westoll (1952) interpreted the skull-roofing bones in terms of contemporary understanding of *D. sussmilchi*. The only specimen known does not retain any of the circumorbital bones, and the lateral-line canals are very imperfectly preserved, so that this was the only possible course to follow. Naturally the inadequacies of the interpretation of *D. sussmilchi* were transferred to *D. lehmanni*. Denison (1968a, fig. 3) has offered a new interpretation based on new information; with this we are in agreement, except for the position of the orbits. These he placed too far forward (Fig. 8).

The suggestion of Westoll *(in* Lehmann and Westoll, 1952) that *D. lehmanni* shows evidence of intracranial kinetism finds no support from our interpretation of its skull roof.

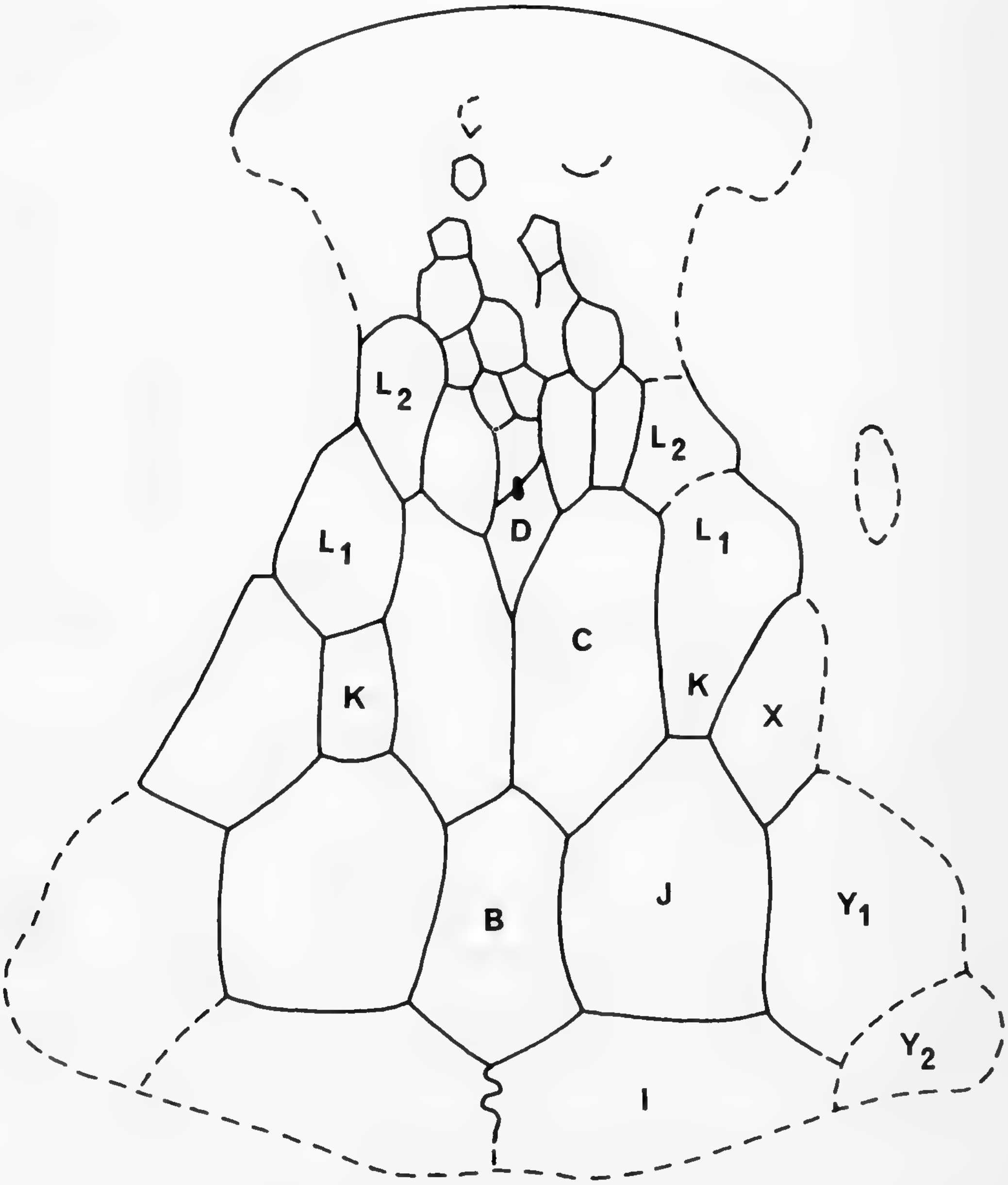


Fig. 8. Skull roof of *Dipnorhynchus lehmanni* modified after Denison (1968b).

The great similarity between the skull roofs of *D. sussmilchi* and *D. lehmanni* is apparent from Denison's figures, and if this alone were considered there would be no grounds for separating them generically. There are, however, considerable differences in the structure of the palates. These are considered in detail below (see Palate).

Uranolophus DENISON. This is the most similar to *Dipnorhynchus* of all the known fossil dipnoans, as is shown by Denison's account (1968a) of the type material from the Lower Devonian of Wyoming (see Fig. 9). The forward position of X and Y_1 with respect to the "eight bones forming a triangular area in the relatively stable posteromedian part of the skull roof" (Denison, 1968a, p. 360), the junction of the I bones behind B, the multitude of small bones in the snout, the absence of a lateral-line canal between bones X and K, and the extension of the supraorbital canal backwards from "K" to "J" are very distinctive features uniting these two genera. *Uranolophus,* however, lacks a pineal foramen, and probably for this reason D is a single stable bone; E is also much larger than any possible homologue in *Dipnorhynchus* and is more like that of *Dipterus.*

The cheek structure of *Uranolophus* has not been described and this is an unfortunate gap in our knowledge. However, Denison's figures 3A, 4, and 5 show enough detail to deduce that the cheek must have been a multiplated complex structure. For example, on his figure 4 the shape of Y_2 and the position of the palatoquadrate (though crushed) show what the shape and position of the operculum would have been; the point of emergence of the infraorbital canal from X

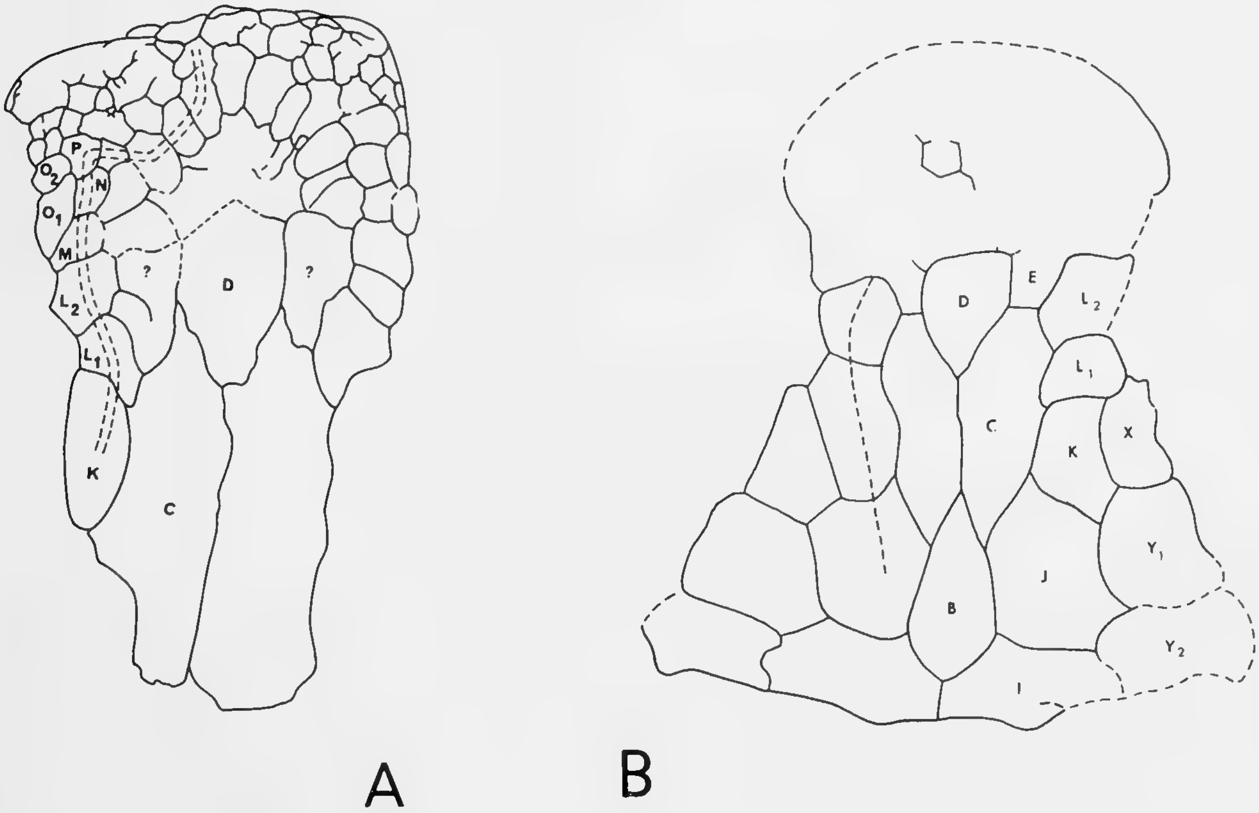


FIG. 9. *Uranolophus wyomingensis.* A) anterior skull roof of specimen PF 3805, Field Museum of Natural History. B) posterior skull roof of specimen PF 1427, Field Museum of Natural History. Redrawn from Denison (1968b).

places the orbit well forward. The outer edges of X, Y_1 imply the existence of two major cheek bones behind 4. On the other hand, the sensory pores on X in figure 5 suggest that the infraorbital canal on that specimen emerged laterally rather than anterolaterally from X, well behind the position of the orbit that can be determined approximately from the position of K. In this case the bone lateral to X receiving the infraorbital canal could not have been a circumorbital and may well have been the homologue of the T of *Dipnorhynchus.*

Dipterus. Further detailed discussion of this genus is unnecessary. Here, for convenience, we summarize the points in which the skull roof of *Dipterus* differs from that of *Dipnorhynchus.* Proportionally the preorbital length in *Dipterus* is much greater; the cheek, the lateral-line series X-Y_1-Y_2, and the non-lateral-line series I-J-K, are relatively shorter; T is completely lost in *Dipterus* and all later genera; the number of bones in the cheek and the length of the cheek are reduced; the bones of the preorbital region are fewer in number and more regular in disposition; the I elements do not meet behind B; H is absent from the extrascapular series; no pineal foramen is present; the bones in the D position are fewer and generally (though not invariably) more regular; O becomes single; the main and the supraorbital lateral-line canals develop a connection between K and X; the lateral-line system on J is reduced to a pit line, which extends on to B; the pit line on I joins with the lateral-line canal on Y_2; the occipital commissure traverses the posterior corner of I rather than passing behind it.

Pentlandia. There are no data on this genus more recent than the account of Watson and Day (1916). The lateral line, the position of the orbits, and the posterolateral corner of the skull are all unknown. However, bone B is readily identified, as also are the paired C and E. The D element has been lost. The lateral-line bones are most reasonably interpreted as in Fig. 10.

Scaumenacia. In general, White's treatment of *Scaumenacia* accords with the principles previously outlined. There are two points of difference between this interpretation (fig. 11) and that of Westoll (1949)—the existence of "K," and the identity of the lateral-line bones adjacent to 2. In all except one of the specimens figured by Westoll (1949, fig. 6) the anterior pit line runs from J to X. This one odd specimen (fig. 6D) apparently has a connection with the plate in front of X on one side, but a normal connection on the other. The unusual side has other peculiar pit line features and can safely be regarded as erratic. We conclude either that the pit line has been captured by X, and K has been lost, or that the plate labelled X by both authors is X + K. The latter alternative can be eliminated since the plate in question is not in contact with C, which is normally developed; moreover, it apparently shows no sign of two centers of ossification. Westoll regards the lateral-line bones anterior to X as the products of a complex set of fusions. The only evidence for his reconstructions is apparently topographical; without other support they must be regarded with caution. White (1965, fig. 36), without comment, goes to the opposite extreme and considers these large bones as single elements. In his single illustration of the genus he labels the element anterior to L_2 as N. In our opinion it is not possible, on the evidence available, to reach a decision on its identity.

Jarvik (1968) has given a restoration of the cheek in *Scaumenacia* showing a short lateral-line canal passing onto 3. This is unknown in any other genus except *Dipnorhynchus.*

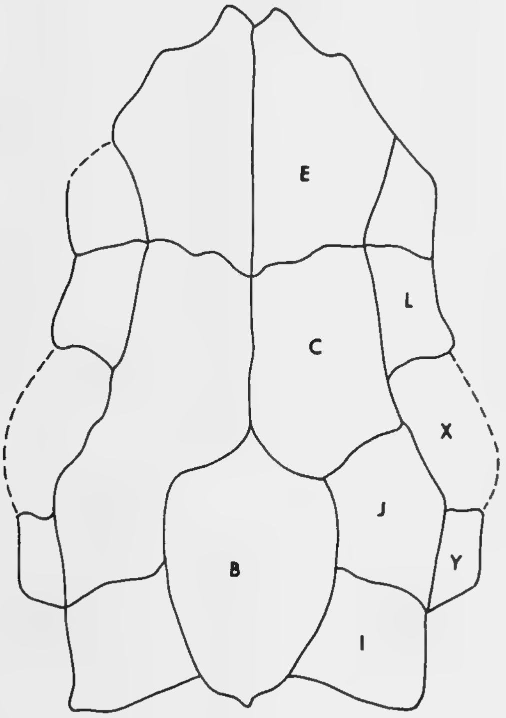


FIG. 10, at left. *Pentlandia macropterus.* Portion of skull roof in dorsal view. Specimen L 10905, Manchester Museum. Redrawn from Watson and Day (1916) with new dermal bone notations.

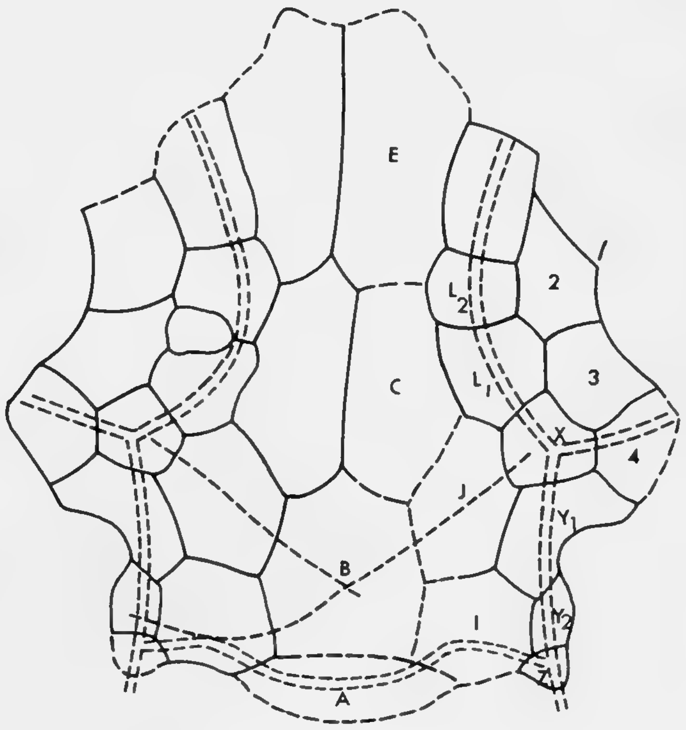


FIG. 11, at right. *Scaumenacia curta.* Portion of skull roof in dorsal view. Unnumbered specimen, Dartmouth College. Redrawn after Westoll (1949) with new dermal bone notations.

Phaneropleuron. As pointed out by Westoll (1949, p. 147), this genus has much in common with *Scaumenacia.* Our interpretation is given in Figures 12A and 12B. There is no reason to doubt the accuracy of Westoll's identification of bone K, except perhaps in his figure 7E where it may be an X; but without knowledge of the position of the lateral-line canals no decision can be reached on this specimen. The large elements anterior to X or K obviously belong to the *L* series, but we cannot determine if L_1 has captured the space occupied by L_2 in earlier forms, or *vice versa.* They are therefore simply labelled L.

Rhinodipterus. It is probable that two different types have been assigned to this genus, *R. ulrichi* Ørvig (Fig. 13A) from the late Middle Devonian which lacks the bone D, and *R. secans* Gross (Fig. 13B) from the early Late Devonian in which D is well developed. The lateral-line series of *R. ulrichi* is known from the type specimen (Ørvig, 1961, fig. 8); contrary to Ørvig's interpretation it is evident that K has already disappeared. A pit line runs from B through J to X indicating a situation in this region similar to that of *Scaumenacia* rather than that of *Dipterus.* On the other hand. White (1962, figs. 1–2) figures a specimen of *R. secans* in which

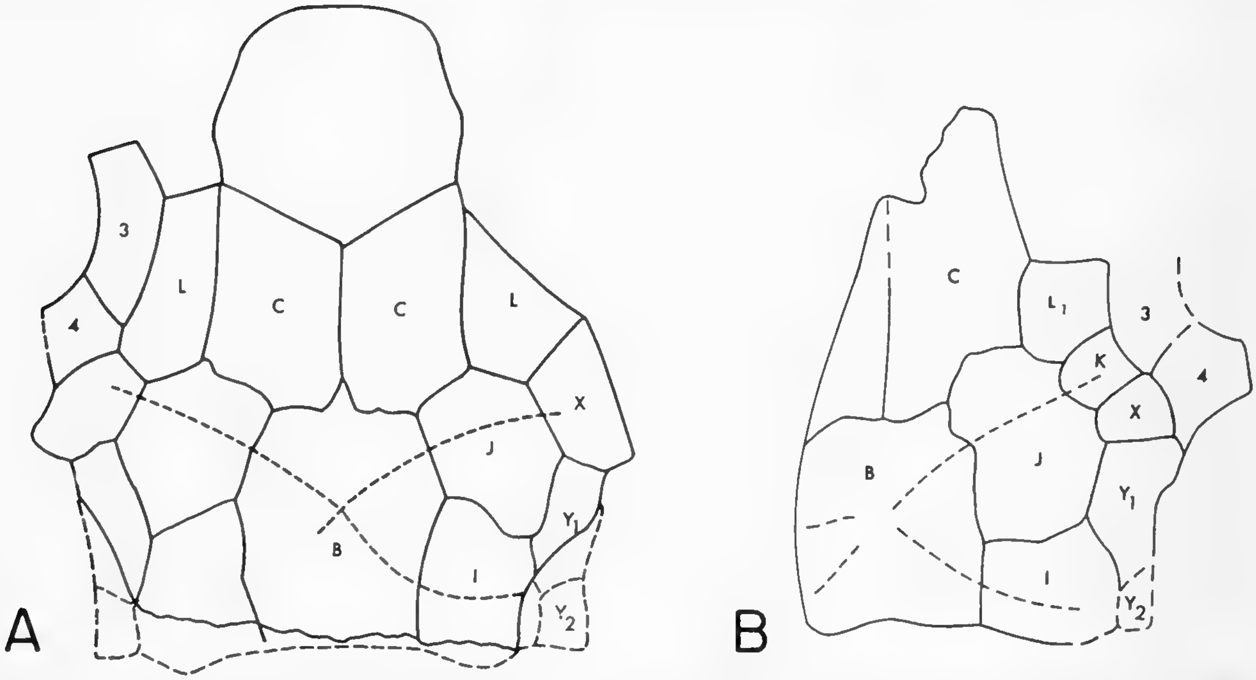


FIG. 12. *Phaneropleuron andersoni.* Portion of skull roof in dorsal view. A) specimen L 10867, Manchester Museum. B) unnumbered specimen, St. Andrew's University Museum. Redrawn after Westoll (1949) with new dermal bone notations.

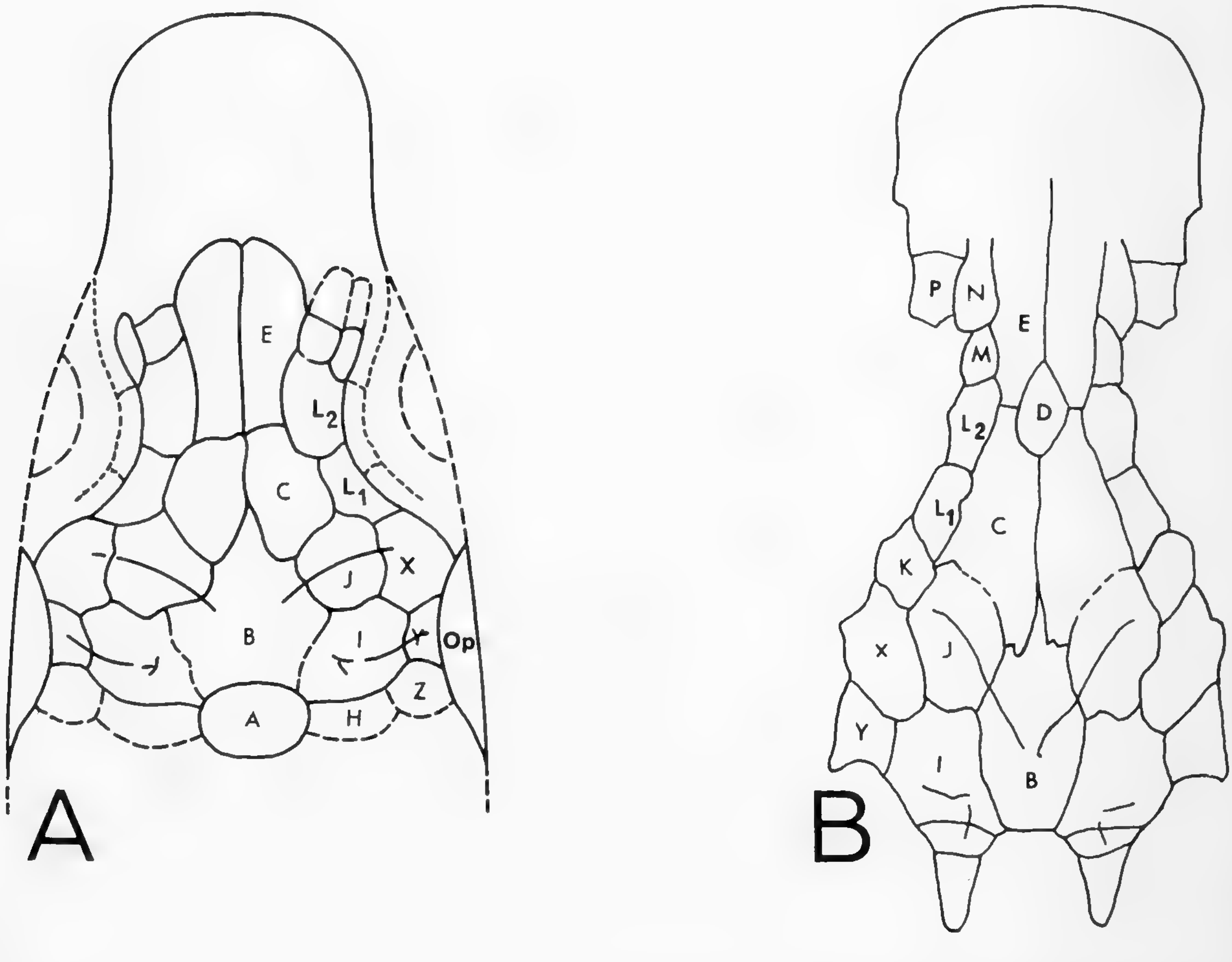


FIG. 13. A) *Rhinodipterus ulrichi.* Skull roof in dorsal view. Reconstruction. Redrawn from Ørvig (1961) with new dermal bone notation. B) *Rhinodipterus secans.* Skull roof in dorsal view. Specimen P 1451, Institut Royal des Sciences Naturelles de Belgique. Redrawn from White (1962) with new dermal bone notations.

K is almost certainly present. We consider that these two species, as described, cannot be congeneric. The main similarities appear to be the elongate shape of the snout, the paired anterior openings in the snout, and the T-shaped structure of the anterior part of the mandible. The anterior openings are not confined to *Rhinodipterus* but have been found also in *Dipterus.* The other two characters are clearly correlated and probably indicate adaptation to the same feeding habit. The long-snouted *Fleurantia* has a similar mandible structure. These similarities therefore seem to be of less systematic significance than the differences in the skull roof. (Note that for White's reconstruction, O must be present in *R. secans* though it is not preserved, thus confirming the identification of that bone by Gross (1956, fig. 13A). Restudy of the genus *Rhinodipterus* is required.

Soederberghia. This is a most illuminating genus in connection with the fate of K (Fig. 14). In it the supraorbital lateral-line canal from J is still fully developed, as also is the anterior pit line. The supraorbital canal joins the main canal in X at the same point as the infraorbital canal. White (1965, p. 23 and fig. 30) regards this bone as the survivor of 'K' or 'X', probably 'K'," but gives no reason for his preference. Perhaps he was influenced by the forward extension of the bone on the

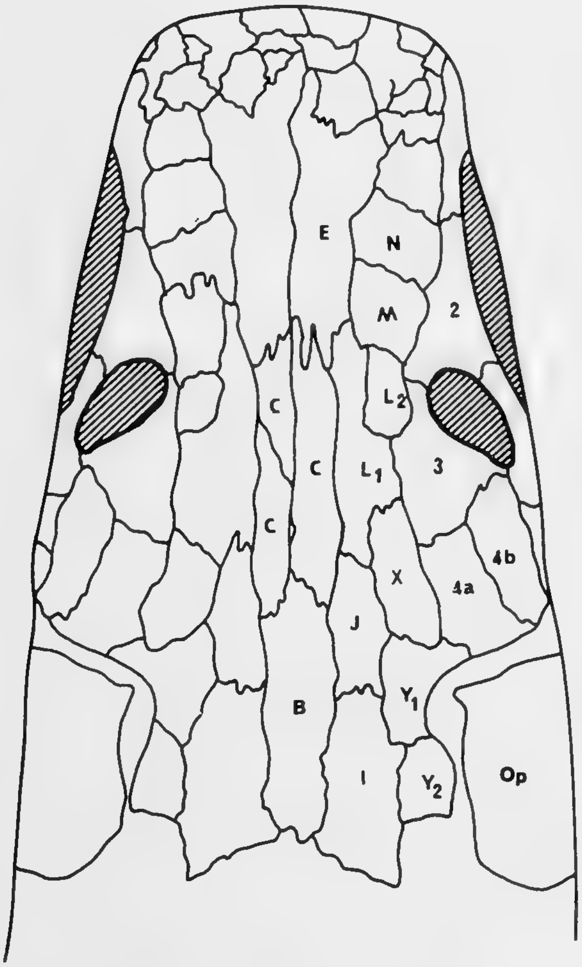


FIG. 14, at left. *Soederberghia groenlandica.* Skull in dorsal view. Reconstruction of the holotype and paratype. Redrawn from Lehman (1959) with new dermal bone notations.

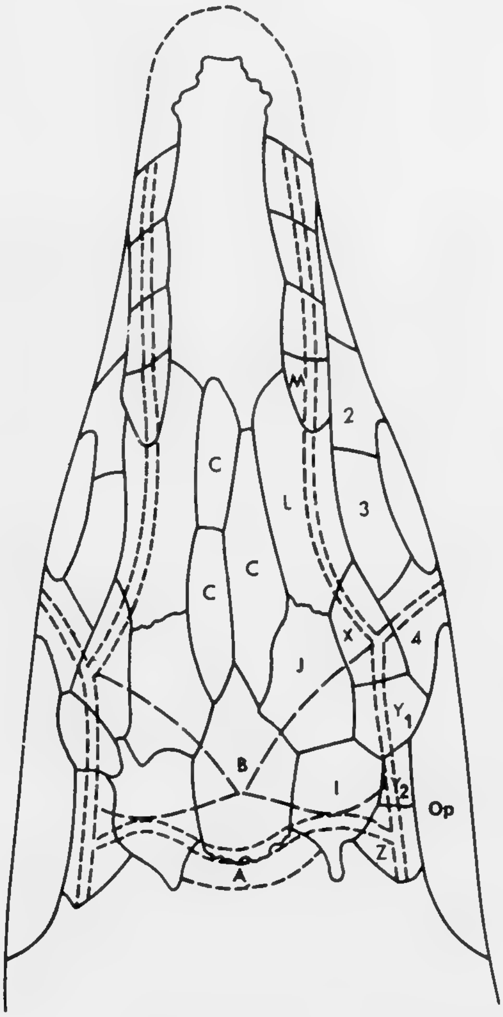


FIG. 15, at right. *Fleurantia denticulata.* Skull in dorsal view. Reconstruction. Redrawn from Graham-Smith and Westoll (1937) with new dermal bone notations.

right side of the specimen shown in Lehman's figure 2 (1959), but that specimen is rather exceptional. Otherwise the bone occupies the normal "K" position, and as the plates of Lehman's work so admirably show, it has a single center of ossification. We regard it as X.

There are two other unusual features of the skull roof of *Soederberghia* that require explanation. In the nomenclature of Lehman (1959), there are two postorbital elements, (the 4A and 4B of our Fig. 14), the upper one of which is not marginal to the orbit. The D bones are very variable, and in different specimens have developed medially, or on the left or right only, or not at all. The M bones also are very erratic. Lehman (1959, p. 20) noted a small plate between the median frontals (i.e., between the two C's), a little behind the orbits. This he referred to as a pineal plate. Occasionally it is missing or a pineal foramen appears to be present. If this structure is properly interpreted it will require a rethinking of the value of relative positions of dermal bones to the anterior elements of the braincase in homological argument. In *Dipnorhynchus, Chirodipterus,* and the living dipnoans the pineal organ stands up dorsally from the diencephalon or is directed slightly forward from it. The diencephalon can thus be inferred (or shown) to be below the anterior part of C or the posterior of D. A similar arrangement in *Soederberghia* would place the diencephalon no farther forward than the posterior parts of C. That this could be so is also suggested by the extreme depression of the skull at the level of, and anterior to, the orbits.

Confirmation of this view would render suspect arguments for dermal bone homologies that paid no attention to the anterior shape of the skull roof. There is no reason, however, to question the use of braincase relationships in determining the homologies of the posterior roof elements; in fact, we consider the position of the pineal organ still to be an open question in *Soederberghia.*

Fleurantia. This genus has much in common with *Soederberghia* in addition to its long head. It has lost K, L is very long and extends up lateral to M, and bones D are irregularly developed. We cannot agree with the interpretation of Graham-Smith and Westoll (1937). Our views are represented in Fig. 15.

CARBONIFEROUS AND PERMIAN GENERA. The system of bone nomenclature used above has been developed for Devonian dipnoans. It has long been recognized that the Carboniferous and Permian members of the group have a different structural arrangement on the posterior part of the skull roof. Chief among these differences are the apparent capture of the occipital commissure of the lateral-line system by B and the movement of Z to a more anterior position. If it is possible to show that these apparent changes are real, then it would be necessary to develop a modified set of definitions for these more highly evolved forms. As an example of how this could be done we will now examine *Sagenodus* (Fig. 16). This genus is well known, shows little variation in the skull-roof pattern, has many features in common with other Late Paleozoic genera, and ranges from the Early Carboniferous to the Early Permian. Therefore it can fairly be regarded as representative.

That B has captured the occipital commissure is generally accepted. The element so labelled (Fig. 16) apparently shows no sign of two centers and still retains

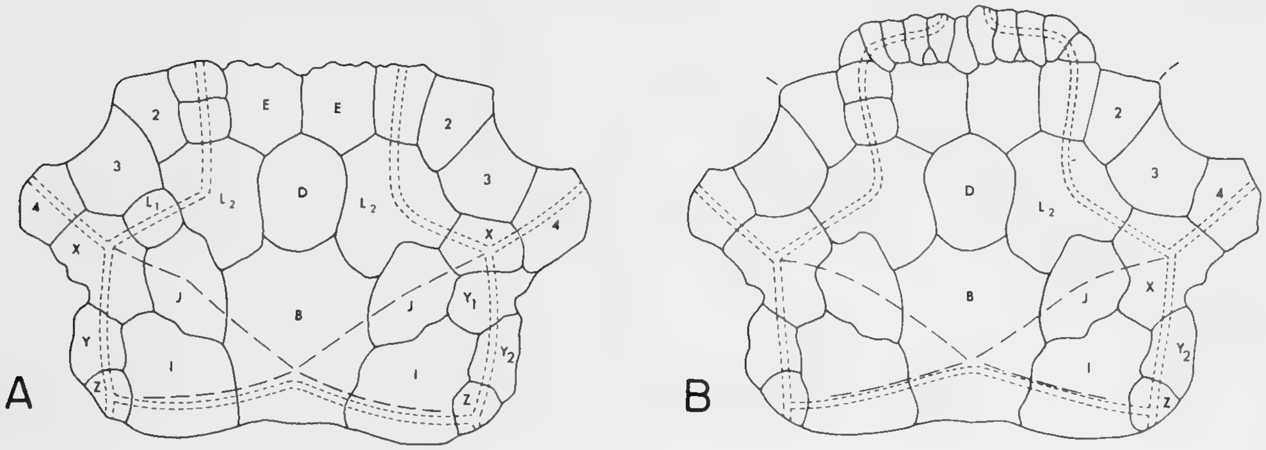


FIG. 16. *Sagenodus*. Skull roof in dorsal view. Reconstructions, showing different conditions of the dermal bone pattern. Redrawn from Westoll (1949) with new dermal bone notations.

both the anterior and posterior pit lines in exactly the same arrangement as the Late Devonian genera *Scaumenacia* and *Fleurantia*. By Late Devonian times the lateral parts of the commissure had already migrated forward from H to I, and it is no surprise to find its median part moved forward to B. Z can still be recognized by the junction in it of the occipital commissure and the main lateral line canal, but it, too, tends to be wedged in between the Y series and I, thus carrying the commissure farther forward. The elements Y_1, Y_2, X, J, 4, and 3, can all be recognized by the same criteria as those for Devonian genera. In Westoll's restoration (1949, fig. 8A-A′) there seems to be evidence from shape (particularly the notch for the articulation of the operculum and the position of the lateral-line canal-anterior pit-line junction), for the fusion of X and Y_1 in some specimens (Fig. 16B). However, Watson and Gill (1923, fig. 1, 2, and 6) show that these bones have a single center of radiation; therefore a more reasonable interpretation is that the space occupied by Y_1 has been captured by X. The fact that X and Y_1 exist independently on one side of some specimens does not affect this argument one way or the other. The position of the palatoquadrate is not known, but we would suspect that, with the incorporation of Z into the fixed series of roof bones, the quadrate ramus would be in contact with Y_2 and Z.

We regard K as absent for reasons given in the discussion on *Scaumenacia*. The bone that lies between J_1 and 3 on the left side of Westoll's figure 8A′ must be L_1 (Fig. 16B). Judging from the radial pattern shown by Watson and Gill on the bones Westoll labels $M + L_2 + K$, we conclude that L_2 has captured the space that in *Scaumenacia* is occupied by L_1, L_2, and M.

The large median bone in front of B is one of the characteristic features of *Sagenodus*. It lies with its anterior edge at about the mid-length of the orbits and its posterior edge approximately in line with the centers of X: that is, it occupies the normal C space. However, it has a single center of radiation and there is no question of its being due to fusion. In most Late Paleozoic genera in which a pair of C elements is developed, D is very small and does not extend forward beyond a line joining the midpoints of the orbits. Therefore it seems that in *Sagenodus* the median bone D has expanded to capture the space that in other genera is occupied by the paired C and D.

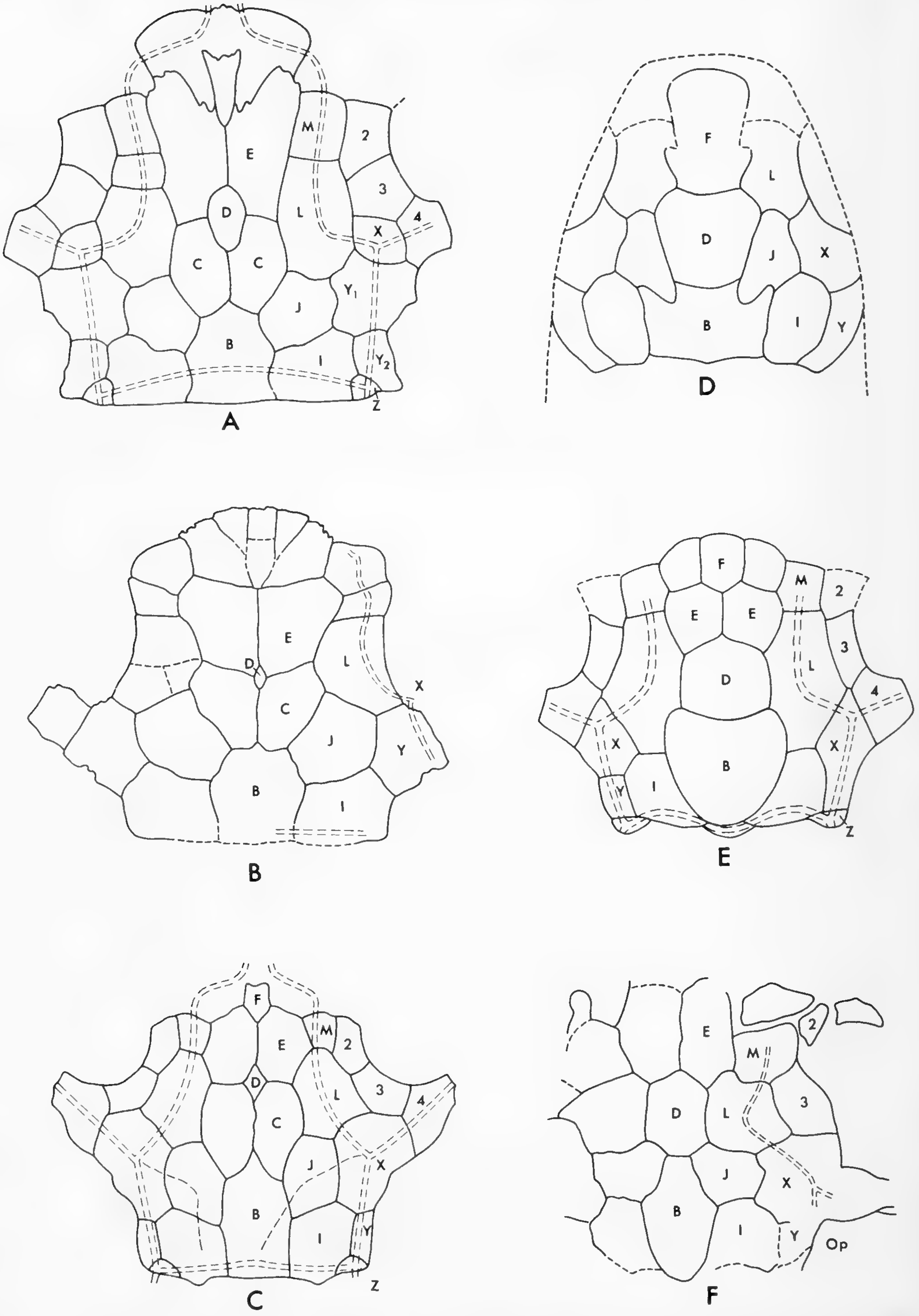


FIG. 17. The skull roof in Late Paleozoic and Triassic Dipnoi, all with new dermal bone notations. A) *Ctenodus*. Reconstruction. Redrawn from Westoll (1949). B) *Tranodis castrensis*. Reconstruction. Redrawn from Thomson (1965). C) *Uronemus splendens*. Reconstruction. Redrawn from Westoll (1949). D) *Paraceratodus geramini*. Reconstruction. Redrawn from Lehman (1966). E) *Conchopoma gadiforme*. Reconstruction. Redrawn from Westoll (1949). F) *Straitonia waterstoni*. Specimen 1891.51.4, Royal Scottish Museum, Edinburgh. Redrawn from Thomson (1965).

Therefore, beginning with the definitions developed for Devonian genera, it is possible to work out the homologies of a Late Paleozoic genus with consistency. Only two of the definitions require modification: B does not lie anterior to the bone containing the occipital commissure, and Z is not loosely articulated.

Analyses similar to the one presented above for *Sagenodus* have also been prepared for the other Late Paleozoic genera *Conchopoma, Uronemus, Ctenodus, Straitonia,* and *Tranodis* with consistent results. These are presented in Figure 17.

THE MANDIBLE OF *DIPNORHYNCHUS SUSSMILCHI*

EXTERNAL DERMAL BONES

The external surface (Figs. 18 and 19) is composed of four infradentary bones on each side and a dentary in front. These are well preserved on specimen P 46773 except on the posteromedial surface. The upper surface of the right side of specimen P 33714 also shows fine detail, but on the Buchan specimen (P 13837) the outer dermal bones are much more fragmentary. Nevertheless, the same number and arrangement of bones can be detected.

Perhaps the simplest approach to these bones is through a direct comparison with *Dipterus platycęphalus* for which Watson and Day (1916) have provided a nomenclature that is widely applied in its original, or a slightly modified, form (Goodrich, 1930; Westoll, 1949; Lehman, 1966; Denison, 1968a). As will be seen below, there are good reasons for believing that the homologies indicated by this nomenclature are correct. The dentary poses no difficulties. It is a relatively long structure compared with that of other Devonian genera, and on the ventral surface is slightly longer medially than laterally. There is no sign of a median symphysis. Its outer anterior surface is well rounded in general, but it carries a shallow groove that arises posterolaterally from the labial pit (Jarvik, 1964) and runs back along its posterior margin. The upper edge of the dentary extends back along the ramus of the jaw for approximately two-fifths of its total length. Just inside its upper edge there is a

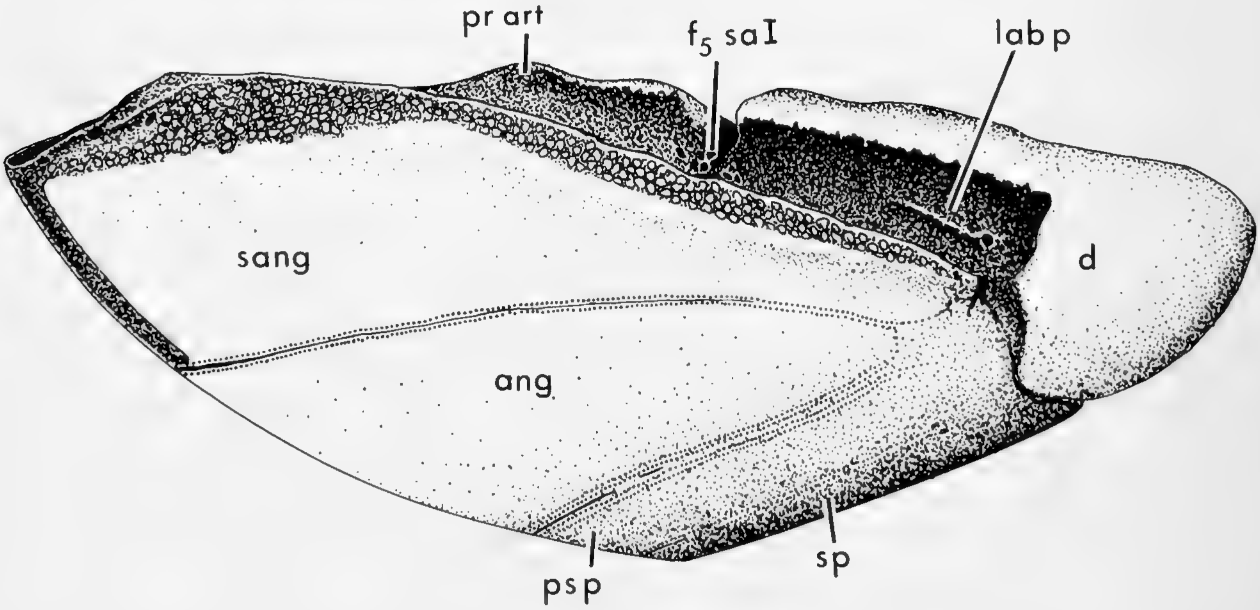


FIG. 18. *Dipnorhynchus sussmilchi*, lower jaw in left lateral view. Based on specimens P 46773 and P 33715, British Museum (Natural History).

shallow furrow that presumably marks its junction with the ossified anterior edge of Meckel's Cartilage. There is a deep incision between the rear edge of the dentary and the prearticular to which it is fused.

The splenials are long, narrow, and subrectangular, the length/width ratio being $^3/_1$ on the P 46773, and approximately $^7/_2$ on the Buchan specimen (P 13837). Their outer edges are slightly arcuate in the Buchan specimen; the width of the bones increases toward the front, where they are in contact with the dentary only.

The postsplenials are longer but have about the same length/width ratios as the splenials. Their outer edges form an outwardly convex arc. Along their anterior edges they are in contact with the dentary, and for a short distance anterolaterally they touch the extremity of the surangular as is shown in Figure 18.

The angular has the outline of a slightly distorted triangle with an obtuse posterior angle against the postsplenial measuring 100°–110°, and the two remaining angles approximately equal. The surface of this bone bulges slightly on both specimens, so that it stands out clearly from its fellows. Its most anterior termination tends to be rounded rather than angular. Both its lateral margins are gently convex outwards.

The surangular has a distorted, elongate, subtriangular outline, but this is modified in various ways. It is greatly produced anteriorly to form a long process that comes in contact with the dentary and the postsplenial; its posterodorsal extremity is truncated to form a relatively straight subhorizontal edge. The whole upper edge of the bone is inflected, the degree of bending being least at the rear, and gradually increasing toward the front of the supra-Meckelian vacuity where it suddenly increases to make the junction with the Meckelian bone underlying the prearticular. This sharper inflection is produced by bending that is almost angular rather than arcuate so that the labial pit, which is in part floored by this surface of the surangular, tends to have a subangular outer edge. The smooth line along the posterior edge of the infradentaries is broken at the junction between the angular and the surangular, the edge of the surangular being set slightly, but distinctly, forward of the general alignment. The whole upper surface of the surangular is covered with small well-rounded beads that are quite densely packed. These seem to have the same structure as the similarly shaped tubercles on the body scales.

On the specimen P 46773, the margins of the separate elements are completely clear throughout. The surangular, angular and postsplenial are separated by sharply defined sutures posteriorly, but these degenerate into a series of large pores anteriorly. They are flanked on each side by two rows of enlarged pores, which presumably are related to Westoll-lines (Fig. 40). The sutures between the two splenials, and the splenials and postsplenials, are not completely preserved. However, they have no median row of enlarged pores anteriorly, and they are marked by two, rather than four, bordering rows of pores.

On the fragmentary Taemas specimen P 33714, the preserved boundaries between the surangular, the angular and the postsplenial are clearly marked, the sutures in places being quite deep.

The sutures on the Buchan specimen (P 13837) are not sharp, but shallow, rounded depressions are present along all preserved bone boundaries. Part of the boundaries between the two splenials and between the splenials and the postsplenials show enlarged pores over part of their length.

Most of the surface of the infradentaries is covered with shiny, densely porous cosmine, apparently identical with that of the skull roof. However, on the anterior parts of the splenials and postsplenials of both specimens the pores disappear. This could just possibly be due to wear, but more probably it indicates a real change in the character of the bone surface (Figs. 55–62). Mention has already been made of the pores that are apparently associated with Westoll-lines on P 46773. On P 33714, both the angular and the surangular show well-developed normal Westoll-lines. On the surangular the lines that are close to the lower and posterior margins can be traced around on the shiny cosmine surface below the beaded upper surface, indicating the separate nature of the cosmine-covered and beaded surface (Fig. 44; Fig. 80).

On the other hand, the surface of the dentary, which is preserved only on P 46773, is not covered with cosmine but "enamel" (see "Bone Histology"). Though it is smooth and shiny, it lacks the dense mat of fine pores, being perforated only by the numerous pores of the rostral tubuli. Viewed under alcohol the dentine layer of bone shows through as a reticulum of "white matter," infilled with "dark brown matter" (Fig. 57). Individual units of the reticulum are 0.05–0.13 mm in diameter. Along the upper posterior crest of the dentary, where an elongate "tooth" is formed, the dentine has a different character again. It is extremely dense and under alcohol shows a much finer reticulum than the remainder of the dentary surface. The units

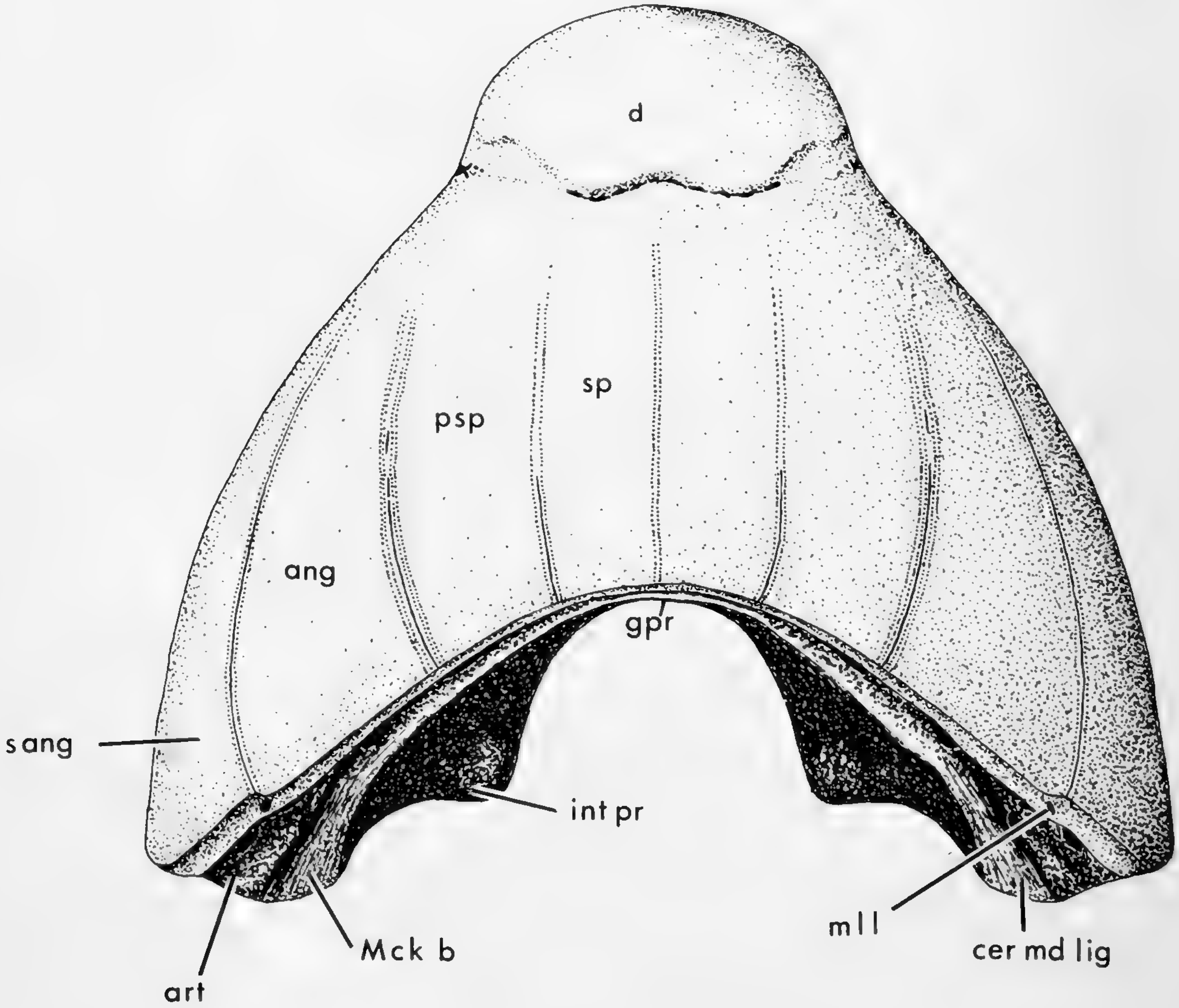


FIG. 19. *Dipnorhynchus sussmilchi*. Lower jaw in ventral view. Same specimens as in Fig. 18.

are 0.03–0.06 mm in diameter. Also, the reticulum is formed of the dark brown matter and the spaces filled with lighter colored matter (Fig. 56). The dentine and enamel surfaces are, in fact, identical with those of the prearticular, a section of which was described and figured by White (1966, p. 7, pl. 1, fig. 1). [Compare also the similar structure on the denticulate edge of the mandible of *Dipterus oervigi* described and figured by Gross (1964).] Along the upper outer edge of the prearticular and dentary, the surface layers are missing and the spongy bone below is exposed (see Figs. 61–62).

THE LATERAL-LINE SYSTEM

The arrangement of the lateral-line canals is clear. They can be traced over most of their courses by natural breaks in the specimens as well as by the positions of the sensory pores. Also specimens P 46773 and P 13837 have been X-rayed, and the canals have shown up with sufficient clarity to enable us to confirm our description.

We have been unable to find a point of exit of the oral canal from the posterior or dorsal margin of the surangular. All available evidence indicates that the canal terminates at, or just behind, the center of radiation of the surangular. There is no posterior connection with any other canal. The oral canal runs forward on the surangular a little above its mid-height, passes along its long anterior process and on to the dentary, though the abundance of relatively large sensory pores in this region suggests that there are probably offshoots into the anterolateral corner of the postsplenial.

The mandibular canal enters the angular in its posterior corner and has a slightly arcuate course on to the postsplenial reaching a point a little posterior to the topographic midpoint of that bone. Here the canal divides into two. The branch forming the mandibular cross-commissure is straight and quite transverse; the anterior branch is also straight, but directed forward so that the two canals lie almost exactly at right angles to each other. Specimen P 46773 is poorly preserved in the region of the medial part of the cross-commissure, but on the right side the branch seems to terminate at the midline of the splenial, though a set of smaller canals radiates anteriorly and anterolaterally from this point. Excavation of a small part of the Buchan specimen (P 13837), however, has shown conclusively that the branches of the cross-commissure do join medially.

The anterior mandibular branch continues forward becoming progressively deeper in the bone (Fig. 52). It passes forward and effects a junction with the oral canal, either just in front of, or behind, the boundary of the "dentary."

On the dentary it has not been possible to demonstrate the course of the canal by X-ray photography. The sensory pores are roughly divisible into two sizes. The larger ones vary considerably in shape from circular to ovate to comma-shaped; they are arranged roughly in two parabolas with their axes directed dorsolaterally (Fig. 40). The upper limbs of the two parabolas meet on the median line, forming a shallow *V*. These do not outline the course of a cross-commissure of the lateral-line canal, as may at first be suspected. They open into the anastomosing rostral tubuli of the symphysial region (see p. 94). The smaller pores are scattered within and lateral to the parabolas and are particularly common around the midline. There are no small pores, however, on the dorsal side of the parabolas.

DERMAL BONES OF THE INNER SURFACE OF THE JAW

The prearticular is a massive bone that dominates the jaw architecture. The dental surface is somewhat differently shaped in the Taemas and Buchan specimens, but the overall similarity is most striking. A rather bulbous prearticular tuberosity (Fig. 20) lies as its anterior extremity opposite the posterior end of the dentary. The tuberosity on the left of the specimen P 46773 is subrounded, but the one on the right is more triangular in outline. On the specimen P 13837 both are much more elongate, and are subrounded in front and taper slightly to the back. Their inner faces opposed the outer faces of the pterygoid elements of the anterior palatal tooth mass, and their posterolateral faces opposed the anterior surface of the lateral tuberosity (see "Palate").

Behind these "teeth" there are the depressions (Fig. 20) that receive the lateral pterygoid tuberosities. Again they are relatively more elongate in the larger than in the smaller specimen, matching the relative shapes and sizes of the adult and juvenile pterygoid tuberosities.

Flanking part of these depressions on each side, and extending posterior to them along the crest of each ramus of the jaw, is an elongated narrow ridge (Fig. 20) that

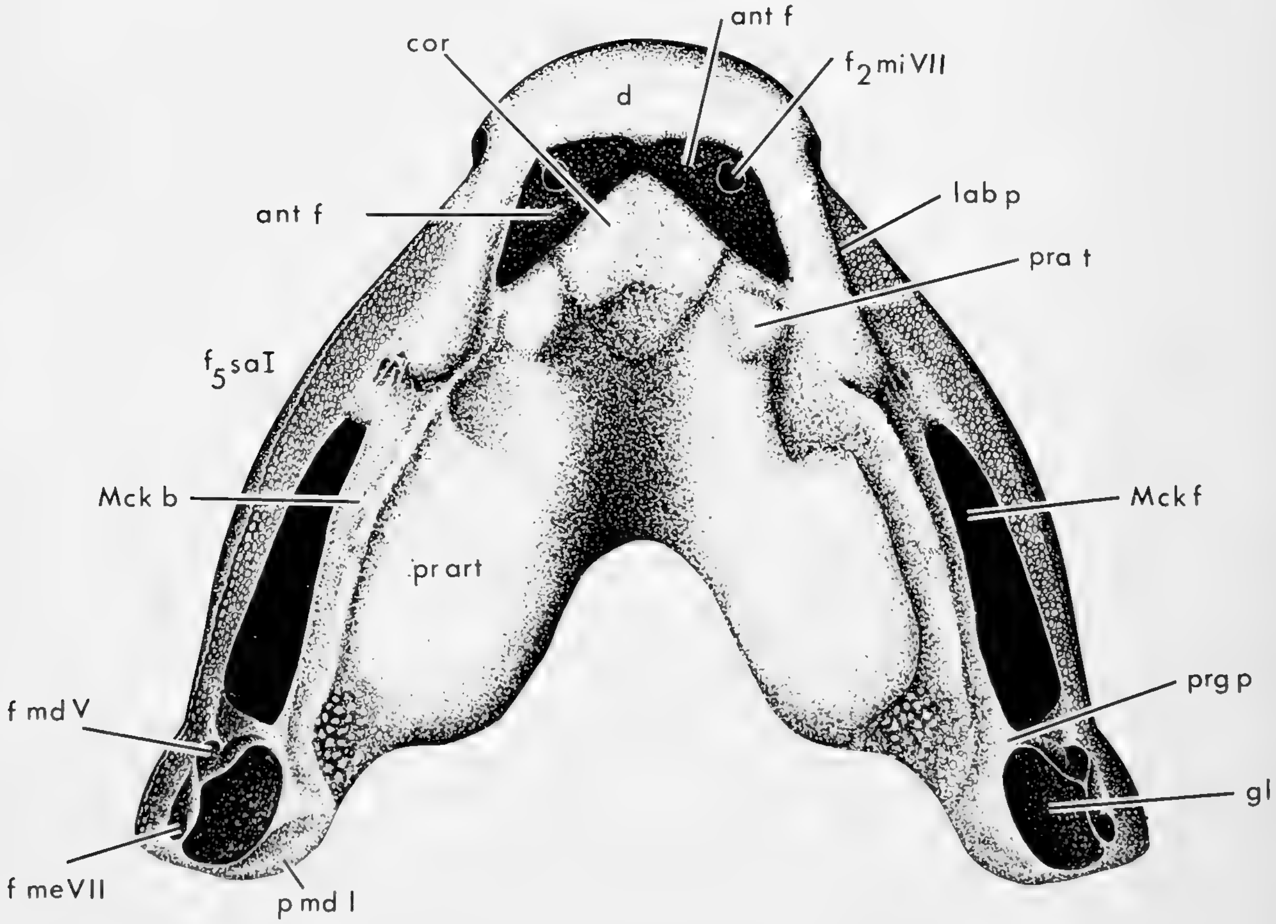


FIG. 20. *Dipnorhynchus sussmilchi*. Lower jaw in dorsal view. Same specimens as in Fig. 18.

forms the dorsal edge of the prearticular. It maintains its height for about three-eighths the length of the supra-Meckelian vacuity, behind which it abruptly loses height and tends to become rather sharper along its crest. It reaches back to a point about three-quarters to seven-eights the length of the vacuity from the front. On the Buchan specimen (P 13837) this ridge is not well preserved on either side, but seems to have had a comparable shape. Inside it on both specimens there is a long lateral furrow (Fig. 20) continuous with the depression receiving the lateral pterygoid tuberosities. It is sharply defined in P 46773 but much less well defined in P 13837. This furrow receives the outer raised edge of the pterygoids when the jaws are shut. The elongate flanking ridge worked against the rather more rounded edge of the pterygoids immediately behind the lateral pterygoid tuberosity.

It is significant that the tubercular lateral surface on the palate of specimen 18815 (Fig. 61) could never have come in contact with this part of the lower jaw, because it is too high up on the palate and around a slight angle.

The inner part of the prearticular forms a large dental surface. It is well and evenly rounded on both Taemas specimens, but is flattened to slightly concave on the one from Buchan, and extends out posteromedially over a subangular prominence (Fig. 19, *int pr*) that gives a very distinctive shape to the jaw. This prominence forms part of the surface of attachment of the very large intermandibularis muscles. The dental surfaces, particularly on the left side, have a subtriangular outline and clearly work against the posteromedian elevations of the pterygoids.

Down the axis of the jaw there is a broad median furrow (Fig. 20) relatively much deeper in the smaller specimen than the larger. This is the median depression of Jarvik (1968), which he interprets as a space for the tongue and for the reception of the basihyal.

All the surfaces of the prearticular mentioned so far are covered with a shiny continuous enamel layer (see previous comment on dentary). A triangular area in the posterodorsal corner of the prearticular, however, has a very rough nodose surface, which is devoid of the enamel layer. This area is rather deeply corroded on the Buchan specimen, but the remnants suggest that it was no different from those on the Taemas specimens, except that it possibly covered a relatively larger area. This surface extends back a little beyond the anterior end of the glenoid fossa and forward beyond the posterior end of the Meckelian vacuity. Its function is not clear.

Posteriorly the dentine shows a rather ragged edge and leaves exposed a large, subvertical, thick wall of "spongy" bone (Fig. 41). In the region of the above-mentioned intermandibular process the bone is 20 mm thick on the Buchan specimen; where it is thinnest it still reaches 7 mm. Along its ventral and lateral edges, this posterior wall of the prearticular forms a tight junction with the thick bar of Meckelian bone previously described.

Forming the anterior part of the interior dermal bones is an element with a triangular anterior outline. This element is probably the representative of the "Md Y" of Jarvik (1967), and the anterior prearticular of Gorizdro-Kulczycka (1950), but might equally be regarded as a fused pair of coronoids. On the Buchan specimen no division between this bone and those behind it can be distinguished, but on P 46773 there is a distinct notched junction at the outer edge and a vague depression toward the midline, producing a rather regular rhombic outline (Fig. 20; Fig. 41). No median suture is visible on either specimen.

Between the coronoids and the dentaries in front is a large deep arc-shaped furrow—the "anterior furrow"—described below. In the Buchan specimen (Fig. 50) the anterior edge of the coronoid is eroded, but it seems probable that it was medially joined with the dentary and formed a thick plate growing out over the Meckelian sheet flooring the anterior furrow and dividing it into two. On the other hand, the anterior furrow is complete in P 46773 (Fig. 41). In it there is only a slight medial projection from the posterior of the dentary toward the acute termination of the coronoid.

The surface of the coronoids meets the anterior pterygoids during mastication, and hence there is complementarity in shape between the two structures. On the large Buchan specimen (P 13837) the coronoids are gently concave overall, but with a slight swelling to the rear. The smaller specimen (P 46773) from Taemas is almost flat anteriorly but quite deeply concave posteriorly.

OSSIFIED ELEMENTS OF MECKEL'S CARTILAGE

The articular is not clearly defined on the Buchan specimen (P 13837), but probably most of it is preserved on the left of P 46773; it is virtually complete on the right of P 33714. Its posterior face, which shows the spongy character of the bone, has a triangular outline and is exposed between the surangular and a bar of dense Meckelian bone. On its upper surface it carries the glenoid fossa, which is approximately 1.4 times as long as it is wide, and shows no sign of being compound (Fig. 20; Figs. 60, 61). The actual articular surface is missing and was, we suspect, formed by a thick cartilagenous pad. In front of the fossa there is a very low, rounded, preglenoid process (partly broken away, Fig. 20) anterior to which the surface of the articular drops away vertically to form the posterior wall of the Meckelian vacuity. The prearticular laps onto the anteromedial corner of the articular.

On the posteromedial side of the glenoid fossa there is a small shelf with the outline of a segment of a circle and with its upper surface striated parallel to its straight edge. It forms the upper face of the bar of dense Meckelian bone referred to above. This shelf lies opposite the similarly shaped and striated surface on the palatoquadrate, and presumably indicates the presence of a palatomandibular ligament. This seems not to have been recorded previously, though in *Neoceratodus* there is a ligament attaching the first visceral arch to the mandible (Greil, 1913, pl. 54, fig. 4). The presence of this ligament in *Dipnorhynchus* cannot be definitely demonstrated, but there are grounds for believing that it may have been present.

In posterior view all specimens show the thick ridge of Meckelian bone lying against the dermal bones and forming the base of the posterior wall of the jaw. This ridge is rather rounded anteromedially, but posterolaterally it broadens and flattens. On the lateral extremity of this flat surface is a slightly differentiated area that may well have supported a ceratohyal-mandibular ligament (see Fig. 19). Much of this flattened surface is delicately striated.

The mesial part of the exposed Meckelian bone on the posterior wall is not only more rounded, as has been mentioned already, but in addition it becomes slightly more prominent. This prominence (Figs. 40, 43; Fig. 53) was probably the site of insertion of the geniocoracoideus muscle. The surface between the intermandibular prominence and the sites of the retractor and geniocoracoideus muscles (Figs. 52, 53) served, no doubt, for the attachment of the intermandibularis muscle. Support for this view can be obtained from the presence in this region of the large foramen that may have contained a branch of the ramus intermandibularis trigeminus that innervates the intermandibularis muscle (see below).

The main ossified element of Meckel's cartilage, which imparts great structural strength to the mandible, forms a thick bar along the inner edge of the supra-Meckelian vacuity and becomes progressively weaker as it extend forward below the posterior end of the dentary. It is this Meckelian bone that would have transmitted the bulk of the stress from the dental surfaces to the articular during mastication. It has a very smooth lateral surface along the median margin of the vacuity where it would have been in contact with the entering adductor mandibulae. On its upper surface, lateral to the ridge on the prearticular (see above and Fig. 20), it carries a shallow furrow that extends back on to the inner side of the articular. In front, this furrow divides into two branches, one extending into the notch between the prearticular and the dentary, and the other into the floor and inner wall of the labial pit (Fig. 40). In this notch there are three or four large foramina, (see below); along the posterior part of the furrow there is a row of similar, but much smaller, nutrient foramina. These demonstrate the presence of soft tissue along the upper surface of the bar, in close contact with the prearticular and the dentary. In the floor of the labial pit there are three more foramina, the most anterior one being in the anterior extremity.

Posteriorly the Meckelian bone rises toward the glenoid fossa where it takes part with the articular in the formation of the low preglenoid process. This process which bears a groove for the mandibularis V nerve (see below) shows no evidence of having been the site of attachment for any part of the adductor muscle.

Lining the medial and anteromedial walls of the Meckelian vacuity is a sheet of Meckelian bone, which thickens considerably toward the mid-line where it fuses with its fellow from the opposite side to produce a powerful vertical symphysical plate. The surfaces forming the medial and posteromedial walls of the vacuity on each side bear a number of more or less vertically arrayed ridges (Figs. 47, 48) which are relatively much more prominent in the Buchan (P 13837) than the Taemas specimen (P 46773). These walls, together with the dorsal wall, also have have numerous impressions of ramifying canals that in places are penetrative. The vertical ridges mark the area of insertion of the adductor mandibulae muscles, and probably of their tendons. This insertion area is extremely large for a dipnoan.

Anteriorly the Meckelian vacuity has a conical termination that extends forward about half the length of the dentary. It is roofed in this region by a thin sheet of Meckelian bone which, in its turn, forms the floor of the very deep arcuate anterior furrow (see above). The Meckelian vacuity is connected to the anterior furrow by a large round perforation (Figs. 20–22; Figs. 46, 50).

The space forward of the Meckelian vacuities and within the curvature of the dentary below the anterior furrow is occupied by a series of coarse, ramifying, bone-sheathed canals (Fig. 54; Fig. 62). These are the mandibular equivalent of the rostral tubuli seen in the snout region and, as previously mentioned, open onto the front of the dentaries at large pores in the enamel surfaces.

FORAMINA AND GROOVES IN THE LOWER JAW

In the following paragraphs we present an account of the various foramina and grooves that mark the bones of the lower jaw in *Dipnorhynchus sussmilchi* (Figs. 21, 22). There are several reasons for making a separate description of these features. They pass between and among different elements of the jaw and are more easily described together rather than piecemeal. Also, the identification of these grooves has been difficult but, we believe, is made easier when the whole vascular and nervous system is considered together. Comparative information on foramina and grooves in the mandibles of other fossil dipnoans is almost wholly lacking (see below, "Comparison"), and therefore we have had to rely almost exclusively upon descriptions of the anatomy of *Neoceratodus* (Greil, 1913; Bertmar, 1959; Fox, 1965) as a guide to the identification of the fossil structures. As will be seen, in large part it is possible to make close comparisons between the nervous and vascular systems of *Neoceratodus* and *Dipnorhynchus*. The reader is advised, however, that these comparisons are wholly provisional. For this reason we have been careful to separate observation from interpretation in the following text.

Lateral and anterolateral to the glenoid fossa there are three foramina that pass vertically downwards into a short wide canal leading into a large chamber (Fig. 21, *ch)* in the outer part of the articular. The largest of these external foramina, or the canal associated with it, is clearly preserved on all three specimens. The other two are definitely distinguishable only on specimen P 33714 from Taemas, although they can be detected on the other specimens with difficulty. The anterior and middle foramina (Fig. 21, *ff md V*) are considered to have carried the mandibular ramus of the fifth nerve which presumably, as in *Neoceratodus* (Fox, 1965) passed downward from the braincase lateral to the masseter muscle giving off several small branches just dorsal to Meckel's cartilage. In *Dipnorhynchus* its passage onto the jaw is marked by a groove across the preglenoid process. Probably, as in *Neoceratodus,* this nerve divided into two main parts, an anterior ramus mentalis V and a posterior ramus intermandibularis V. We consider a groove (Fig. 21, *gr mV + VII)* leading forward from the large chamber in the articular (seen in P 13837) to have carried the r. mentalis V forward on the inner side of the surangular in the wall of the Meckelian cavity.

The third dorsal foramen *(f me VII)* leading into this region is in the correct position to receive the ramus mentalis externus VII (see below, "Braincase"); this probably branched within the mandible along with the ramus mentalis V. It is suspected that it may have continued forward to some of the rostral tubuli, but this cannot be demonstrated.

Leading directly backward from the common chamber in the articular is a broad canal emerging on the posterior face of the mandible between Meckel's cartilage and the margin of the surangular at a large foramen (Figs. 21, 22, *f int V*). This foramen shows evidence for the passage of three elements (Figs. 51, 52). A large posteroventral embayment in the foramen passes into a groove that runs ventrally down the junction between the Meckelian bone and the surangular and angular; a smaller posterodorsal embayment runs posteriorly. These probably carried the anterior and posterior branches of the ramus intermandibularis V that had branched off from the ramus mandibularis V within the chamber in the articular bone. A still smaller dorsal groove within this common foramen runs along a shallow furrow between the articular and surangular and then off the mandible lateral to the glenoid fossa. Its function is unknown.

On the posterior face of the mandible, in the junction between the articular and the posterior band of Meckelian bone, is a foramen (Figs. 21, 22, f_1 *sa I*) with a sharp ventral edge, but with a well-defined furrow in its upper edge (P 46773 and P 33714) or its upper external edge (P 13837). This furrow is continuous with an indefinite groove (Fig. 21, *gr ea I*) that runs along the outer face of the articular just behind the surangular, and then dorsally off the mandible. Internally this foramen opens into a canal that passes between the articular and the posterior band of Meckelian bone to emerge in a large foramen (Fig. 22, f_2 *sa I*), high on the inner lamina of the Meckelian vacuity, immediately below the knobbled surface of the prearticular. These two foramina are interpreted as having carried the superior branch of the first efferent arterial arch. The main arch presumably passes down the back of the mandible. Internally the superior branch runs forward in a distinct groove sending off a strong dorsal branch a short distance in front of the foramen and a ventral branch from a point a little further forward. It then proceeds anteriorly in a broad arc beneath the flat prearticular dental surface. The ventral branch runs along the upper surface of the symphysial septum and enters a foramen (Fig. 21, f_3 *sa I*) in the anteromedial wall of the Meckelian vacuity. From here it is distributed to the canals in the bone below the anterior furrow, some of which are connected with the sensory pores on the dentary. The main canal enters a large foramen (Fig. 21, f_4 *sa I*) situated almost directly below the posterior end of the dentary. From here canals are distributed within the bone to smaller foramina in the posterior ends of the labial pit and the anterior furrow (Fig. 21, ff_5 *sa I* and ff_6 *sa I*). Over most of its course, the groove appears to be double, and it possibly also carried a branch of the seventh nerve. Forward from its posterior dorsal offshoot it gives rise to several tiny, almost imperceptible, grooves that are anterodorsally or anteroventrally directed. From the dorsal branch of the main groove, two very shallow grooves run forward along the bar of Meckelian bone forming the margin of the supra-Meckelian vacuity and enter small foramina in the anterior edge of the vacuity.

The large foramen f_1 ea I is possibly the one labelled *c.ly* by Jarvik (1967, pl. 1, fig. 2) in *Neoceratodus* and interpreted as a lymphatic canal (following Ruge). In P 46773 especially (see Figs. 40, 43) this foramen is entered by two grooves, a broad vague one across the Meckelian bone from the direction of f_1 sa I and a much narrower one along the edge of the dermal bones from f int V. The former probably carried the first efferent branchial artery and the latter a branch of anterior ramus intermandibularis V. It is possible that a branch of the seventh nerve could also enter this foramen. In specimen P 13837 the main groove comes into the dorsal edge of the foramen, but this is probably due to the fact that the artery passed a little further posterodorsally than in the other specimens. From f_1 ea I the artery, and presumably the nerves, are carried forward into the mandible through a short canal and along a groove in the inner surface of the angular and then up into the front of the Meckelian cavity to emerge in one large and several smaller foramina (Figs. 21, 22, ff_2 *ea I*). These serve the complex ramifying system of the rostral tubuli that occupies the space between the thin sheet of Meckelian bone and the dentary, below the anterior furrow.

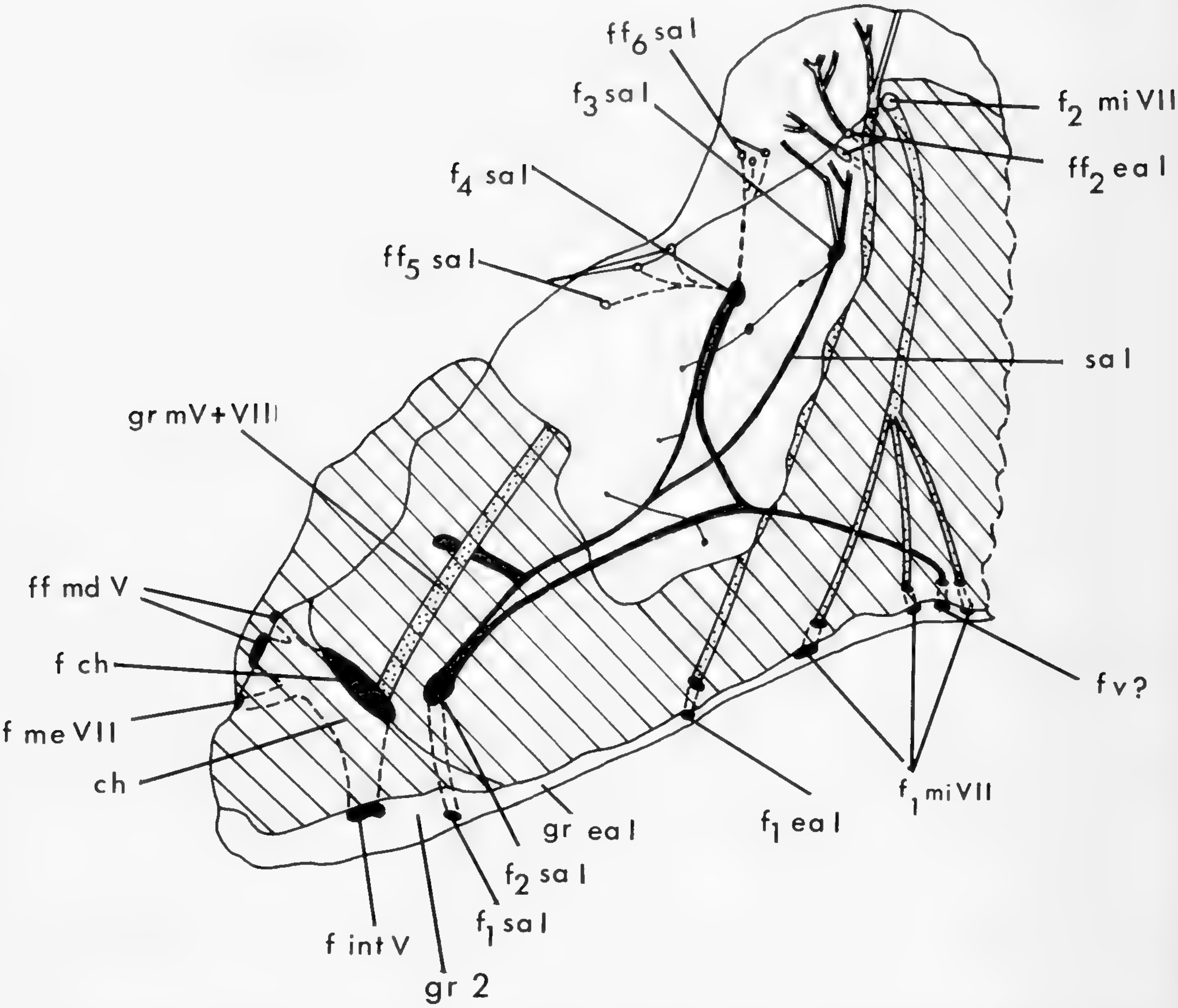


FIG. 21. *Dipnorhynchus sussmilchi.* Ventrolateral aspect of lower jaw. Specimen P 13837, National Museum, Melbourne. Semidiagrammatic representation of vascular and nervous foramina and grooves in the jaw. Solid black indicates structures in or on Meckelian bone, stippling indicates grooves on the inner surface of external dermal bones.

Finally, on both sides of P 13837 there are four small foramina situated on the posterior face of the mandible near the junction between the postsplenial and splenial and the Meckelian bone. (On the left side there are apparently only three foramina on the external surface, but one large foramen apparently provides access for two canals.) In P 46773, a smaller specimen, there are only three foramina in this position on the right side. The same is probably true of the left side though it is too broken to be certain of this. Three of the foramina in P 13837 and two in P 46773 (Fig. 21, f_1 *mi VII)* lead forward through short canals onto grooves uniting on the internal surface of the postsplenial, approximately at its center, and then pass forward as a single groove opening via a large foramen *(f_2 mi VII)* into the anterior furrow. The function of this system is not clear but the foramina are too small to have carried arteries or other vessels. They may well have carried one or more branches of the ramus mentalis internus VII and possibly such a nerve as the ramus alveolaris VII. The fourth foramen in P 13837 and the third in P 46773 (Fig. 21, *fv?)* is larger and is connected to a vertical canal that issues in a foramen

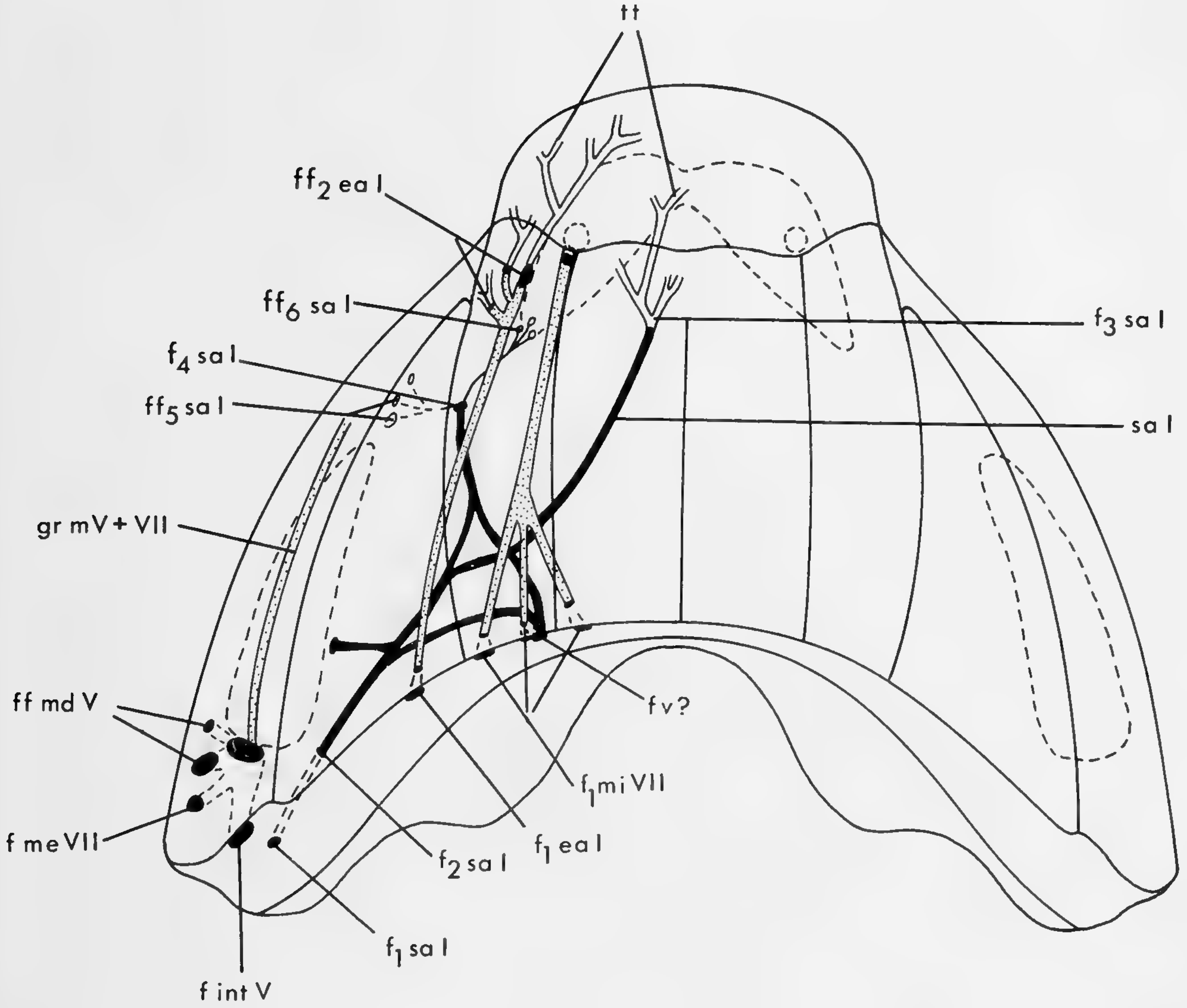


FIG. 22. *Dipnorhynchus sussmilchi*. Attempted reconstruction of the canals, foramina, and grooves for the nervous and vascular systems of the lower jaw.

on the posterior wall of the Meckelian vacuity. This then continues as a groove passing laterally and vertically till the bone begins to arch over to cover the undersurface of the prearticular dental surface. Here it branches. The posterodorsal branch runs back below the previously mentioned groove for the superior branch from the first efferent artery and sends off several short shallow grooves that enter foramina. The anterodorsal branch, which is stronger, crosses the groove for the artery and fifth nerve and then swings anteriorly to run adjacent to the main branch of the same. They enter the bone together (Fig. 21, f_4 *sa I*). From here, as mentioned previously, canals are distributed to the posterior ends of the labial pit and the anterior furrow. This system may have held vascular elements.

We have said nothing of the venous system, but judging from Fox (1965) there is no reason why the lateral venous sinus should not enter the jaw through the Meckelian vacuity and a branch may pass out posteriorly through the chamber *(ch)* and the dorsal notch in the foramen f int V.

COMPARISON WITH OTHER DEVONIAN GENERA

The construction of the mandible of *Dipnorhynchus* is more massive than that of any other known dipnoan. This massive character is achieved by a relative increase of the length of the symphysial region so as to give a greater ventral surface area; but a greater thickness of the Meckelian bone, particularly those parts forming the upper rami of the jaw and the medial symphysis; and by a greater thickness of the dermal bones throughout. Only two other genera have mandibles of comparable shape and strength—the Lower Devonian *Uranolophus* (Denison, 1968a) and the Upper Devonian *Holodus* (Gorizdro-Kulczycka, 1950). However, in neither of these genera is the length of the symphysis relative to the total mandibular length as great as in *Dipnorhynchus*. One would expect to find a correlation between the strength of the jaw and the size of the adductor mandibulae muscles, and hence in the size of the supra-Meckelian vacuity. It is of interest, therefore, to note that in both *Uranolophus* and *Holodus* the supra-Meckelian vacuity is large in comparison with that of *Dipterus* (Jarvik, 1967), but in neither does it reach even half the size of that of *Dipnorhynchus*.

All three of these genera with unusually massive jaws have a specialized nonceratodont dentition, indicating adaptations to peculiar diets. In the case of *Dipnorhynchus* this seems to have been mainly shellfish, and consequently the strength of both bones and muscles is not unexpected. It is clear that though later dipnoans may have had smaller adductor pits, it is not correct to attribute this character to all Devonian genera, particularly the earlier ones (cf. Jarvik, 1967, p. 439).

Melanognathus canadensis Jarvik. This is a recently described dipnoan genus (Jarvik, 1967) concerning which there are problems. Jarvik (1967) gives the age as Lower Devonian but doubt has been thrown upon this by Denison (1968a) who believes it to be possibly no older than Middle Devonian. The main difficulty concerns the structure of the single known specimen—a pair of lower jaws preserved flattened out and showing only the external surface. Because of the potential importance of this specimen we have borrowed and restudied it.

The surface of the dermal bones is covered by a thick shiny cosmine layer such as is often found in Devonian dipnoans and also osteolepid rhipidistians. The cosmine layer bears the openings for the lateral-line organs of the oral and mandibular lines that meet with their fellows of the opposite side in the symphysial region. There is also a cross-connection between the two lines arteriorly on each side. If for the moment we disregard the possible dermal-bone pattern, the arrangement of the lateral lines is quite similar to that in *Dipnorhynchus*.

Jarvik (1967) described the external dermal-bone series in the jaw of *Melanognathus* as being made up of four roughly rectangular bones arranged in a square pattern. A complicated terminology was required for these elements because they seemed so completely different from those of other dipnoans. Jarvik (1967) suggested that this curious pattern in *Melanognathus* was primitive and the one from which all other dipnoan patterns had evolved.

Restudy of the specimen shows, however, that the separations between bones "MdOcl" and "MdMcl" and between these two and "MdOc2" and "MdMc2" are in fact irregular cracks in the cosmine layer. They are not symmetrical on the two jaw rami and there is no evidence of sutures in these positions. The separation between "MdOc2" and "MdMc2," where there has apparently been some slight resorption of the cosmine, is more clear and includes a definite suture. We have been able to find no definite indication of any other suture in the specimen, even by the use of stereoscopic X rays. We therefore cannot at present assign *Melanognathus* to any position of importance in the phylogeny of the dermal bone patterns of Dipnoi. Our safest interpretation of the scanty evidence is that the element "MdOc2" of Jarvik's description probably represents part of the large surangular of *Dipnorhynchus,* while "MdMc2" is the major portion of the angular. (While this study was in progress Dr. H-P Schultze of Göttingen kindly showed us his own re-assessment of *Melanognathus* (now published, 1969) which, though differing in details from ours, is in essential agreement as to the major features of the jaw and the absence of sutures anteriorly defining any "MdOcl" or "MdMcl" elements.)

Uranolophus. Uranolophus shows a pattern of dermal bones basically similar to that of *Dipnorhynchus,* though it seems to be more variable. No definite surangular has been observed, but Denison (personal communication) reports that the surface in the surangular region is not well preserved on any specimen, and this may well account for its apparent absence. Another apparent difference that may be of importance is Denison's record (1968a, p. 378) of "grooves in the cosmine which resemble incomplete sutures" on the ventral symphysial region of one specimen. These grooves "divide this area partially into what appears to be a mosaic of small plates." On the other hand, a *Dipnorhynchus*-like pattern of splenials and postsplenials is shown on the posterior part of the symphysial region of another specimen. It is conceivable that *Uranolophus* indicates the fusion or enlargement of the dermal bones from an ancestral mosaic *after* the separation of the dipnoan and rhipidistian stocks, as was suggested by Denison. However, in view of the tentative nature of the observations, and the similarities between the mandibular bone patterns of *Dipnorhynchus* and primitive Crossopterygii (see "Discussion;" Fig. 24), we remain very dubious of such a conclusion. A further interesting feature in which *Uranolophus* resembles *Dipnorhynchus* is the presence of a deep anterior furrow which is apparently also floored by bone of Meckelian origin (the symphysial plate of Jarvik). No foramina have been observed in this plate, and no rostral tubuli have been noted, though both may well be present. The preglenoid process is short, smooth, and apparently carries a foramen equivalent to the one labelled *f md V* in *Dipnorhynchus,* together with a similar groove that passes inward across its upper surface. Thus, apart from the obvious differences in detention, there is a striking similarity between the mandibles of these two genera.

Dipterus. Because of the significance that has attached to the structures of the jaw of *Dipterus* since the work of Watson and Gill (1923), and the central position given to it in the recent discussion by Jarvik (1967), we have re-examined the two specimens that have become more or less classic, namely L 10858, Manchester Museum, and 53370, Geological Survey, London. In addition, we have prepared another specimen from Caithness (53377, Geological Survey, London). A new reconstruction has been prepared (Fig. 23) and the new specimen is shown in Figs. 63–67.

The anterior parts of all specimens are crushed and it is difficult to be certain of the bone boundaries. However, a median suture and sutures separating splenials from postsplenials can be distinguished posteriorly on L 10858 and 53377. In addition, each of the three specimens is cracked on at least one side in a position that would correspond with the suture between the postsplenial and the angular, while on the right side of 53377 the suture itself can be observed. This, taken in conjunction with the evidence cited by Watson and Gill (1923, p. 208) from a specimen in the Royal Scottish Museum, places the existence of splenials and postsplenials beyond reasonable doubt. The sutures in this region fade away anteriorly, a feature

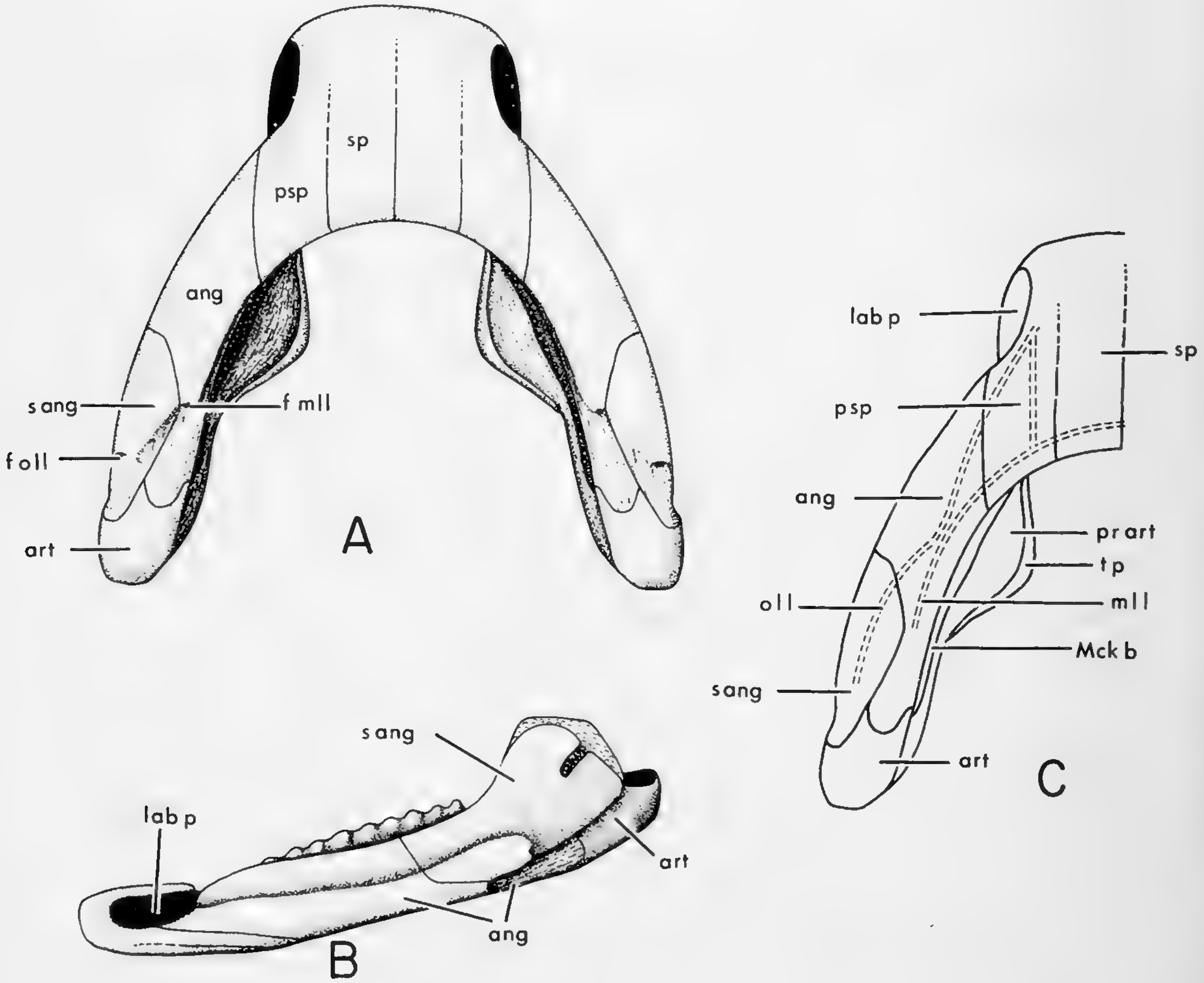


FIG. 23. *Dipterus valenciennesi*, lower jaw. Specimen 53377, Geological Survey, London. A) restoration of the lower jaws in ventral view. B) lower jaw in right lateral view. C) right mandibular ramus in ventral view; diagrammatic, showing the courses of the oral and mandibular lateral-line canals.

that is also shown by the *Dipnorhynchus* material. No suture separating off an element such as the "MdOc1" of Jarvik (1967), and no suture between the dentary and the outer dermal elements behind it, can be observed. The existence in *Dipterus* of "MdOc1" postulated by Jarvik is considered conjectural. The suture between the postsplenial and the angular apparently reaches the edges of the labial pit, but there is no evidence of its position beyond this. Presumably the postsplenial must take some part in the formation of the wall of the labial pit, and if this is so, it is the only part of the splenial or postsplenial without a cosmine cover. The angular ("MdOc2Mc2" of Jarvik) is a large thick bone extending from the labial pit in front to a contact with the articular behind. Its outer surface consists of three parts. The upper (or vertical) portion forms the anterior edge of the supra-Meckelian vacuity and is devoid of cosmine. The median (or horizontal) portion forms an abruptly rounded junction with the upper portion and occupies the major part of the surface. It is cosmine covered and terminates abruptly directly below the deepest part of the adductor pit. Extending back from here along the ventrolateral surface of the articular is the very much smaller third portion. It has no cosmine and must have been deeply buried beneath the skin. The mandibular lateral-line canal must have passed over its surface since it enters the bone in the posterior corner of the cosmine covered median portion, as shown by Jarvik (1967, text-fig. 6A; pl. 5, figs. 1, 4: mc). It is this third portion that Jarvik labels as Meckelian bone (Meck.) on his pl. 5, fig. 1, though he apparently interprets it as dermal bone on all his text figures. A cut through the ramus of 53377 (Fig. 67) shows the angular to be almost triangular in cross section. The bulk of the bone is coarsely spongy, but its inner face is formed of a moderately thick layer of darker-colored denser textured bone with very few coarse cavities. It is the posterior extension of this layer that forms the third portion referred to above.

All three specimens show the presence of Jarvik's "MdOc3," the surangular. It is a relatively small element only the anteroventral third of which is cosmine covered. Posteriorly and dorsally the bone covers the outer face of the articular. In its posterodorsal edge there is a notch, probably for the ramus mentalis externus facialis. The oral lateral-line canal enters via a notch in the posterior edge of the cosmine covered surface. The internal structure of this bone is the same as that of the angular.

The lateral-line canals are essentially as they are figured by Jarvik (1967, text-figs. 6A and 7B) so far as we can determine. Unfortunately it has not proved possible to check out their precise course without the destruction of a specimen. However, from the cut in specimen 53377, natural breaks, and the distribution of pores, it has been possible to confirm the position of the whole system except the junction between the mandibular and oral canals on the postsplenial. One feature in which *Dipterus* is different from *Dipnorhynchus* is the depth to which the canals are buried in the bone. In *Dipterus* (Figure 67) they lie almost against the dense inner bone layer and open to the surface through large pores that tend to splay out from the canal. This accounts for the relatively wide scatter of the pores on the bone surface.

Meckelian bone is exposed on the posterior face of the jaw above the inner edge of the angular. It is fragile and crushed on all specimens examined. The prearticular on the other hand is a dense, strong element. Posteriorly it lies against the inner face of the articular as shown in Jarvik's text-figure 6B. Anteriorly it extends for-

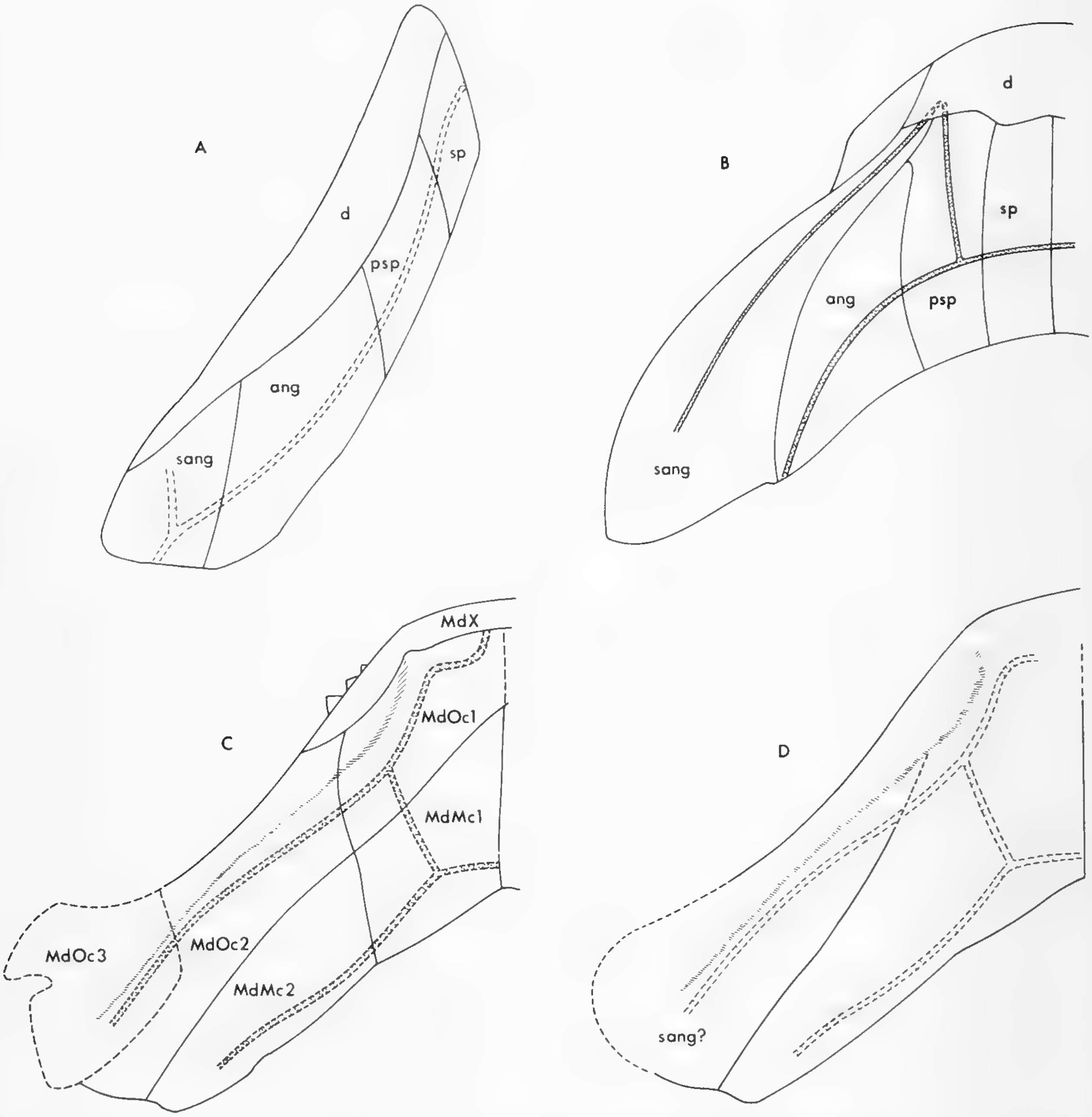
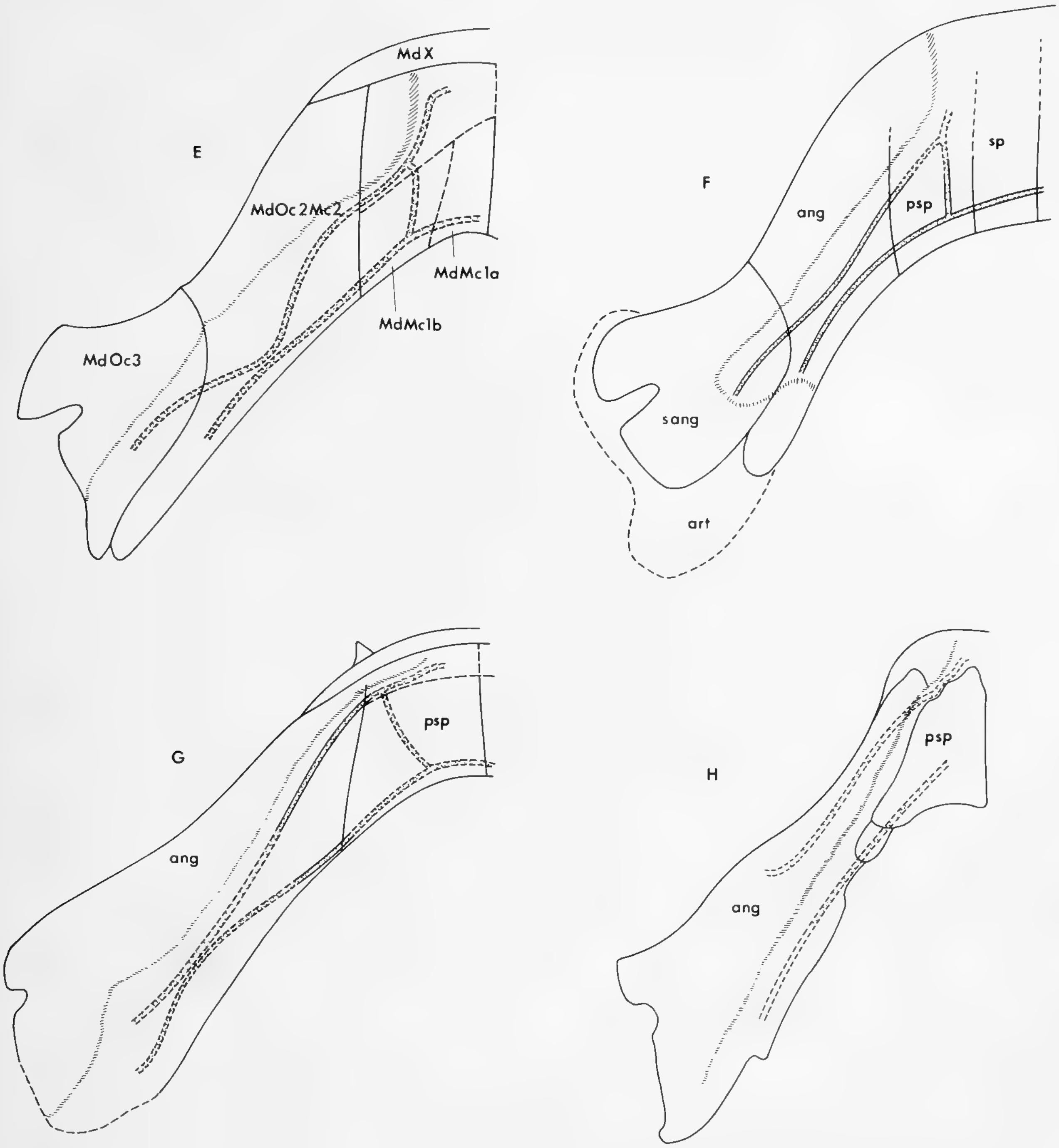


FIG. 24. Dermal bones of the mandible in Rhipidistia and Dipnoi. A) *Holoptychius* (Crossopterygii, Rhipidistia), after Jarvik and various sources. B) *Dipnorhynchus sussmilchi*, original. C) interpretation of *Melanognathus* given by Jarvik (1967), redrawn. D) new interpretation of *Melanognathus*. E) interpretation of *Dipterus* given by Jarvik (1967). Redrawn. F) new interpretation of *Dipterus*. G) *Scaumenacia cura*, redrawn from Jarvik (1967), new interpretation. H) *Neoceratodus*, redrawn from Jarvik (1967), new interpretation. E, F, G, and H appear on p. 61.

ward above the splenial and postsplenial where it unites with its fellow and is supported by the median symphysial wall of Meckelian bones. This region is not well preserved on any specimen, and we find it almost impossible to reconstruct with accuracy. There does, however, seem to have been an anterior furrow in the curve of the dentary, and this must have been floored with thin Meckelian bone. Rostral tubuli may be present in the snout of 53377, but the evidence is not conclusive. There are, however, large pores in the dentary similar to those that open into rostral tubuli in *Dipnorhynchus*.

Apart from obvious differences in detention, the mandible of *Dipterus* differs from that of *Dipnorhynchus* in the following main features. The angular and sur-



angular are relatively much thicker and have a large inflected upper surface devoid of cosmine. We see no reason to believe that the inflected portions are remains of a separate pair of oral canal bones. The surangular is much shorter than in *Dipnorhynchus,* and the oral canal emerges from its posterior edge. This abbreviation of the surangular means that the oral and mandibular canals must be carried forward through the angular; since it is a single bone both canals must be present in the primordia. This, rather than bone fusion or replacement, accounts for the merging of the canals in this bone. Further expansion of the angular at the expense of the surangular, and its final elimination, leads (Fig. 24) to the condition seen in *Scaumenacia* (Jarvik, 1967, text-fig. 5B). The Meckelian bones in *Dipterus* are not nearly so strong as those of *Dipnorhynchus:* stresses were presumably transmitted through the jaw along the thickened outer dermal bones as well as the prearticulars.

In this connection it is important to note that the small Meckelian vacuity permits a strong contact to be made between the prearticular and the angular in front, and both prearticular and surangular are strongly attached to the articular at the rear.

Rhinodipterus. Apart from the highly specialized *Griphognathus,* the only other Devonian genus for which the external dermal bone pattern is reliably known is *Rhinodipterus.* Gross (1956, p. 26–27) and Jarvik (1967, p. 161–165) have described *R. secans* (Gross) in some detail from the single known well-preserved specimen. Though there are obvious differences related to the very large labial pits, there is a clear similarity between this genus and *Dipterus.* This can be well seen from a comparison of our Fig. 23 with Gross' text-fig. 18. The "Infradentale 1" probably contains both splenial and postsplenial elements; "Infradentale 2 and 3" corresponds with the angular and "Infradentale 4" with the surangular. Of particular interest are the lack of cosmine on the upper and posterior surfaces of the angular and surangular, the position of entry of the mandibular canal into the angular, and the foramen for the ramus mentalis externus facialis high on the surangular against the preglenoid process.

Mandibles of the later Paleozoic genera *Sagenodus* and *Ctenodus* are known, but no useful comparison with *Dipnorhynchus* can be made.

We conclude from this survey that the splenial, postsplenial, angular and surangular are primitive dipnoan features; that there is no evidence for fusion of primitive oral and mandibular series of bones; that the transition from the *Dipnorhynchus* type of jaw structure to the *Scaumenacia* type can be readily explained by the progressive elimination of the surangular and the splenial, the space occupied by these bones being captured by the angular and postsplenial (Fig. 24); that the tendency of mandibular and oral canals to run together in the angular in *Dipterus* and *Scaumenacia* can be readily explained by space capture of this type; and that one of the most striking features of the mandibles of the Early and Middle Devonian dipnoans is the essential similarity of their elements of construction despite gross differences in size and shape.

PALATE AND BRAINCASE OF *DIPNORHYNCHUS SUSSMILCHI*

PALATE

Dermal Bones of the Palate. The ventral aspect of the palate (Fig. 25; Fig. 72; Figs. 74, 75, and 77) shows a pair of partially separate anterior pterygoid elements and posteriorly a complete unbroken bone surface lacking sutures, superficially sculptured into a series of depressions and elevations. A small hypophysial opening is present in the posterior portion of the palate. Specimen P 33699 (Fig. 26; Fig. 73) shows internal and dorsal parts of the palate. In the quadrate region of three specimens (P 33699, 18815 and F 10813) there is a marked shelf behind the posterior edge of the dermal palate, where the ventral surface of the visceral palate is exposed and presumably reveals the separation between dermal and visceral portions.

As shown by P 33699, the dermal part of the palate seems to be formed in two halves, fused in the midline. These must be the principal pterygoid elements, to which separate anterior pterygoids (Fig. 25) are attached anteriorly. There seems to be no indication of the presence of a median parasphenoid element. The pterygoid elements are intimately fused to the visceral portion of the palate. Cross sections of the palate show that the occlusal surface is formed of a layer of dentine (possibly with superficial "enamel") resting on a basal mass of spongy bone. There is no lamellar bone present and the cross sections give no indication of a separation between visceral and dermal units. On the sides of the palate the dentine surface is continued dorsally a short way and then breaks up into a series of small irregular tubercles (Fig. 79). The external surface of these tubercles may be seen, in cross sections, to be continuous with the external surface of the ventral palatal surface and is distinct from the dorsal and lateral surfaces which lack the dentine layer. The tubercular area along the lateral margin of the palate is therefore a region where the dentine layer is interrupted, either through phenomena of growth or (also) because this marks the limit between the skin of the palate and the naked occlusal surface. As we shall later see, the ventrolateral margins of the palate did not form a part of the actual occlusal surface.

The ventral surface of the palate is marked by the previously mentioned depressions, ridges, and elevations which form the only kind of "teeth" in *Dipnorhynchus.* The posterolateral margin of the palate bears a well-marked lateral ridge (Fig. 25, *lr*), separated by an anteroposteriorly directed lateral groove (Fig. 25, *lgr*) from a large posteromedian elevation (Fig. 25, *pmel*) that meets its fellow from the other side in front of the hypophysial opening. The hypophysial opening lies in a shallow, roughly triangular depression formed posteromedially of the two posteromedial elevations just mentioned. Anteriorly, the lateral ridge runs toward a large

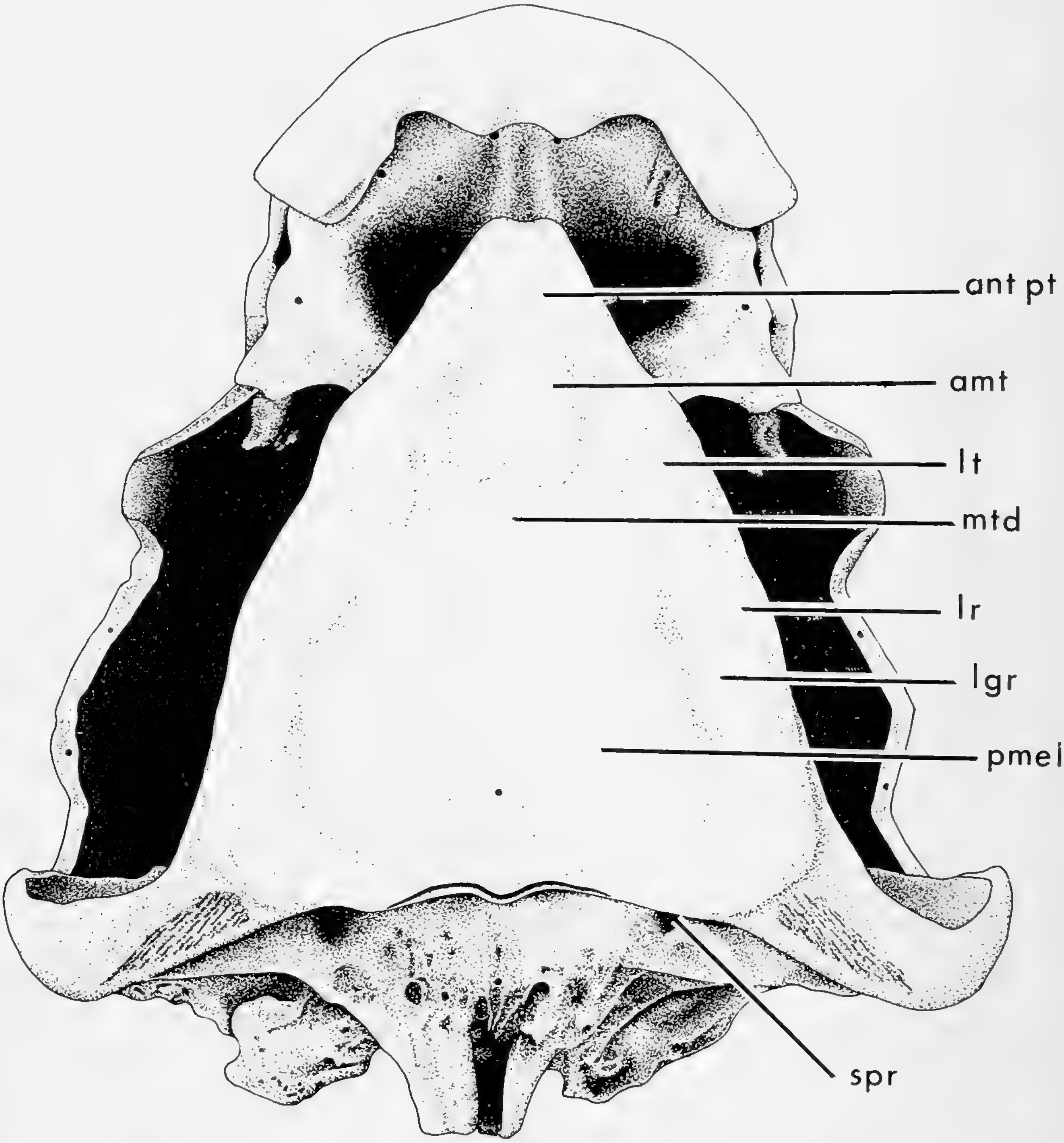


FIG. 25. *Dipnorhynchus sussmilchi.* Palatal view of skull. Holotype.

lateral tuberosity (Fig. 25, *lt*) but is separated from it by a forward extension of the lateral groove that here reaches laterally to the margin of the pterygoid. The lateral tuberosity is very prominent and is anteriorly elongated where it makes a slight bulge in the lateral margin. The lateral tuberosity is partially separated from the large posteromedian elevation by a median extension of the lateral groove that curves round to meet the one from the opposite side in a very shallow transverse depression (Fig. 25, *mtd*). Where the pterygoids meet in the anterior midline there is a large anteromedian tubercle (Fig. 25, *amt)* which fuses with its fellow from the opposite side. This median tuberosity has the appearance of being a single structure in specimen F 10813A, but its paired nature is clearly seen in 18815 and P 33699. The anteromedian tuberosity on each side is located slightly in front of the lateral tubercle and is separated from it by a well-marked deep anterior depression. In specimen P 33699 the anteromedian tuberosity of the right side is considerably larger than that on the left. Presumably this reflects both some abnormality in the occlusal pattern with the mandible and the double nature of the

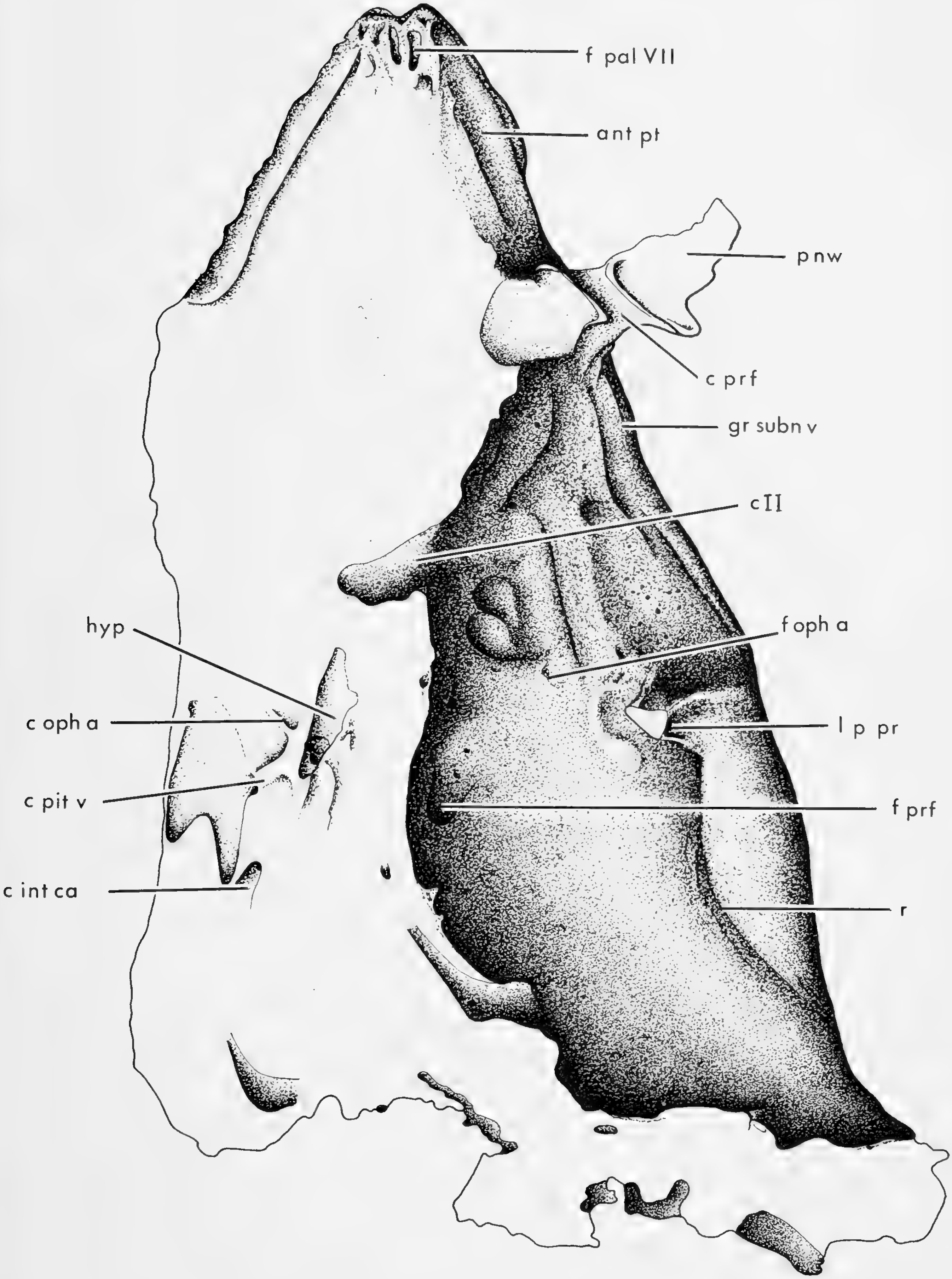


FIG. 26. *Dipnorhynchus sussmilchi.* Dorsal view of detached palate. Specimen P 33699, British Museum (Natural History).

coronoids. In one specimen (18815, Fig. 74) a further anterior tuberosity is present in the midline anterior to the anteromedian tuberosity. This is not present in the other specimens. In specimen P 33699 there is a slight transverse groove in the anterior face of the anteromedian tuberosity that may indicate the coalescence of the two tubercles. The anterior pterygoid (the homology of which is uncertain) has the shape of a narrow strip of bone attached to the anterolateral margin of the pterygoid and reaches in front of the principal pterygoid to meet its fellow from the opposite side. In the largest specimen available (P 33699) there is a triangular space separating the two structures (Fig. 72). This cavity is not present in the other specimens; we presume that in life it was filled with cartilage that for some reason was not calcified in this particular individual. The occlusal surface of the anterior pterygoid is covered with a thin layer of dentine exactly like that of the principal pterygoid. Apart from being gently rounded ventrally it does not form any specially modified dental surface. In specimen P 33699, the occlusal surface of the right anterior pterygoid is flat and on the left side it is very slightly grooved. The functional significance of the variation in shape and curvature of the occlusal surfaces between the three available specimens is not clear. That it is not simply a function of age is demonstrated by the fact that 18815 and F 10813A are of approximately equal size. On the other hand, P 33699 is considerably larger and seems more worn although the dentine layer is apparently intact. There is an interesting problem here with respect to the wear, growth, and replacement of the occlusal surfaces. If separate vomerine elements were present, they are not preserved in the materials studied.

VISCERAL PALATE. The visceral and dermal sections of the palate in *Dipnorhynchus sussmilchi* are fused together in a single mass and, as previously noted, it is difficult to see distinctions between the two portions. It is also difficult to determine the separation between visceral and neurocranial elements in the holostylic skull. However, the optic nerve foramen must be enclosed wholly in neurocranial material, and we may surmise that the separation between visceral and neurocranial elements is at a level ventral to this foramen. Specimen P 33699 is a palate of *Dipnorhynchus* that has become broken away from the neurocranium. As may be seen in Figs. 26, 27, and 73, the specimen includes the ventral margin of the optic nerve foramen and canal and the hypophysial recess, but is morphologically ventral to the endocranial cavity proper. This specimen shows the entire dorsal surface and most other features of the visceral palate.

The line of separation between the visceral palate and neurocranium may be presumed to pass ventrally to the postnasal wall (the ventral portion of which is closely associated with the visceral palate), and the optic nerve foramen. Posteriorly it may be concluded that ascending and otic processes of the palate are incorporated in the side of the braincase (see "Braincase" and "Embryological Analysis"). Ventrally the two halves of the visceral palate are fused in the midline, enclosing the hypophysial recess (Fig. 26), behind which is presumably the morphological position of the basal palatal articulation—here entirely obscured by the complete fusion of palatal and braincase elements. The palate is not continued posterior to the basal region and the posterior margin of the palate forms a distinct vertical "step" in this region.

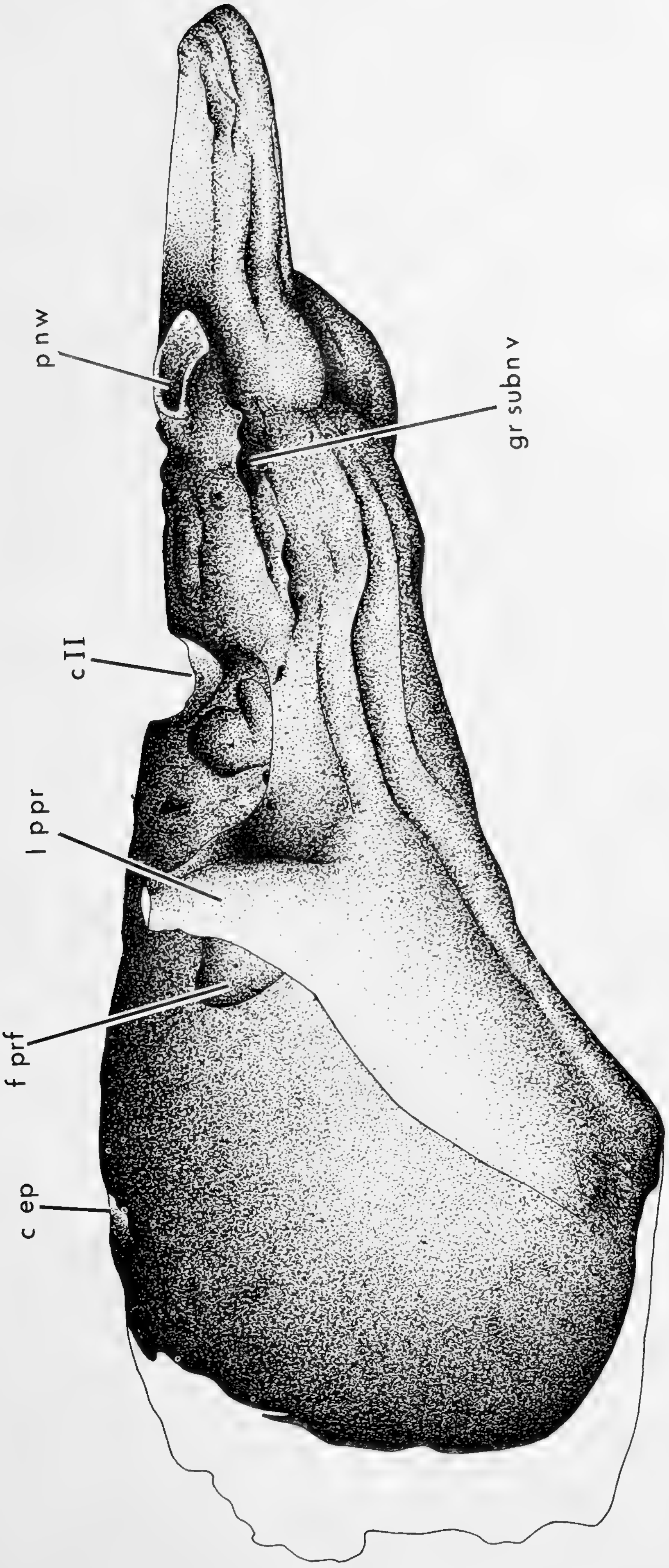


FIG. 27. *Dipnorhynchus sussmilchi.* Right lateral view of detached palate. Same specimen as in Fig. 26.

The visceral palate seems to form two special buttressing regions in the palatal-braincase contact. First, there seems to be a buttress of the palate under the root of the postnasal wall; second, there seems to be a thickening of the visceral palate immediately anterior to the optic nerve foramen (Fig. 26) forming a region of firm palatal-braincase union. A third interesting feature of the visceral palate is a stout conical vertical projection located on the lateral part of the dorsal surface of the palate at a level immediately behind the optic nerve foramen. This "lateral palatal process" (Figs. 26 and 27) seems, in fact, to separate the orbital and temporal chambers of the skull laterally. Its function is obscure. It does not attach to the dermal skull roof nor does it, as far as we can see, form the attachment for any major muscle system. A similar structure is found only in *Uranolophus* among the Dipnoi.

The dorsal surface of the palate posteromedial to the lateral palatal process is an extremely smooth (osseous) surface. This smooth surface extends posterodorsally over the endocranium and forms the floor of the adductor chamber, the extent of which is discussed below ("Braincase"). The floor of the orbital chamber, anterior to the level of the lateral palatal process, is marked by muscle scars, probably for eye muscles (Fig. 26) and a series of foramina for vessels. There is a special concentration of extremely small foramina in a triangular area on the lateral part of the palate, immediately anterior to the lateral palatal process. The internal connections of these various foramina have been determined by radiographic methods. As shown in Fig. 28 and Fig. 94, there is a complicated network of canals for nerves and blood vessels passing through the substance of the palate. A canal for the carotid artery enters the braincase in the otic region and then passes forward to the hypophysial cavity. In specimen P 33699 this canal has a brief connection with the canal for the hyomandibular ramus of the seventh nerve that passes downward through the wall of the braincase from the trigeminofacialis ganglion complex. A narrow canal for the ophthalmic artery (Fig. 28, *c oph a*) passes anterolaterally from the hypophysial recess and opens in the orbital cavity somewhat behind the optic nerve foramen. The distal half of this canal forms a distinct ridge in the dorsal surface of the palate before opening slightly anteromedial to the dorsolateral palatal process (Fig. 26). A larger canal passes almost directly anteriorly from the front of the hypophysial recess. Just in front of the level of the optic nerve foramen this canal divides, one portion continuing directly forward to open in the space between the principal and anterior pterygoids. This canal probably carried a palatal artery. The second branch of the main canal (Fig. 28, *vc*?) turns slightly laterally to run to a point behind the postnasal wall where it opens at four different foramina (Fig. 28; Fig. 94). This second canal is very wide in the material at hand. We do not know what vessel it may have carried. There is also an indication of a wide canal running laterally along the palate just medial of the lateral palatal process. This canal opens at a foramen anteromedial of the lateral palatal process, but again its exact significance cannot be determined. Just in front of the postnasal wall, a large foramen in the lateral margin of the palate leads into a rapidly branching system of minuote canals and probably carried venous elements laterally from the palate. In addition, there is a marked groove along the lateral surface of the palate in the nasal region. This is interpreted as having carried a large subnasal vein posteriorly from the nasal region (see p. 72).

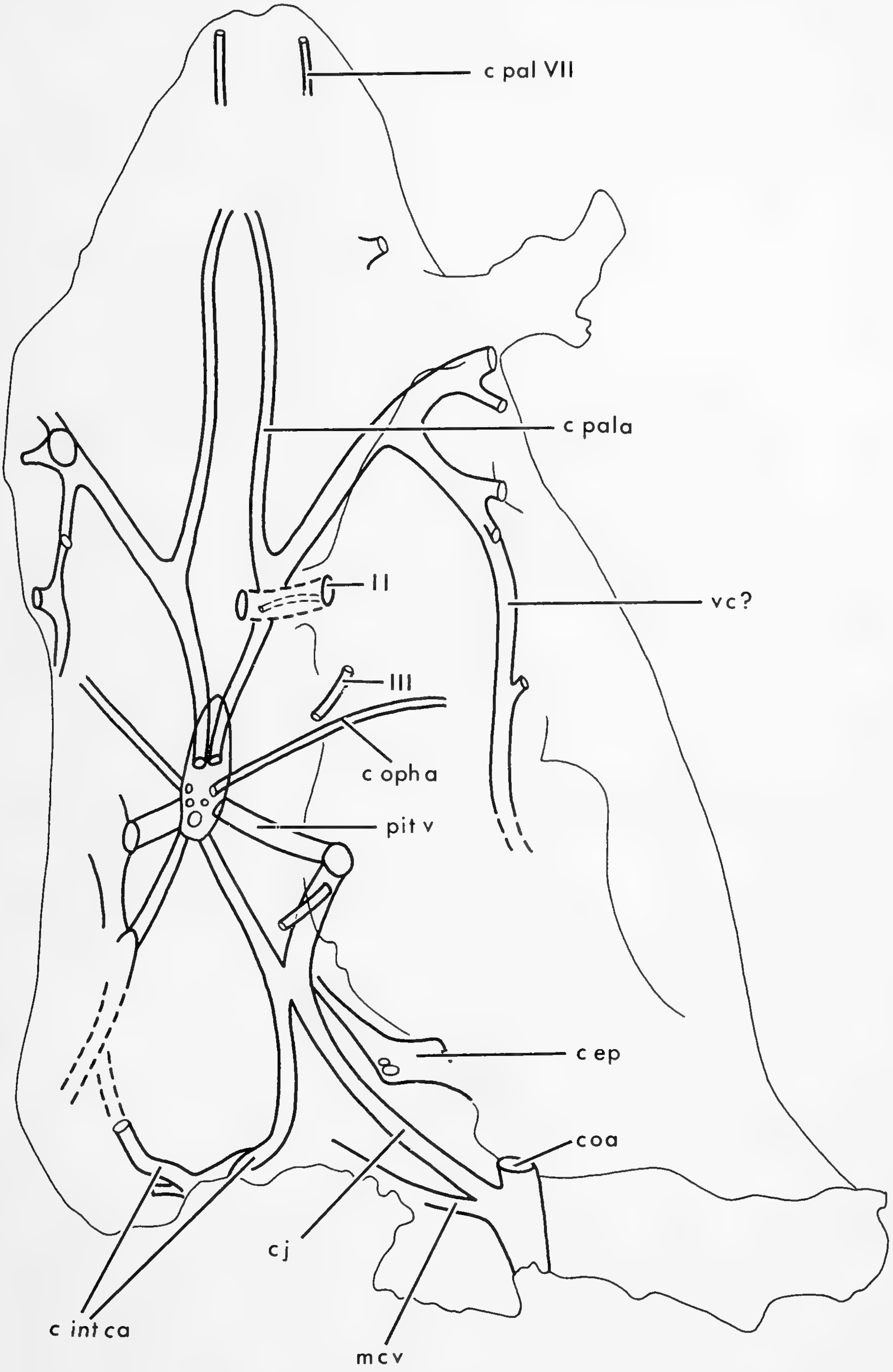


FIG. 28. *Dipnorhynchus sussmilchi.* Palate in dorsal view showing the courses of various nerve and vascular canals as revealed by direct examination and X-ray photography. Same specimen as in Figs. 26 and 27.

BRAINCASE

As has already been mentioned with respect to the palatal structures, there is considerable difficulty in distinguishing between neurocranial, visceral and dermal elements in the skull of *Dipnorhynchus sussmilchi*. In the following descriptions an arbitrary distinction has been made in most cases. For convenience the braincase will be discussed under four separate headings: nasal, orbital, temporal and otic, and occipital regions.

NASAL REGION. In the material at hand, all portions of the original osseus nasal capsule seem to have been preserved. The floor of the capsule and a ventral part of the internasal septum, if present, were apparently only cartilagenous in life.

There is a complete dorsolateral nasal capsule pierced only by foramina for blood vessels and nerves, as discussed below. Externally, only the dermal covering of the snout may be seen. The "upper lip" curves markedly around the ventrolateral margin of the snout and a short "shelf" of dermal bone thus separates the nasal region from the tip of the snout. The nasal openings are therefore wholly ventrally directed. The space between the dermal bones of the tip of the snout and the anterior perichondral wall of the nasal capsule was apparently occupied by endochondral bone (not preserved) in which the delicate perichondral rostral tubuli ramify. These are shown in Fig. 69. The external openings of these tubuli are seen in the enamel-covered portion of the snout. Internally they connect with the nasal cavity through two large and several very small foramina (Fig. 29, *cc m V*).

A notch in the margin of the bony "upper lip" (Fig. 29) clearly marks the position

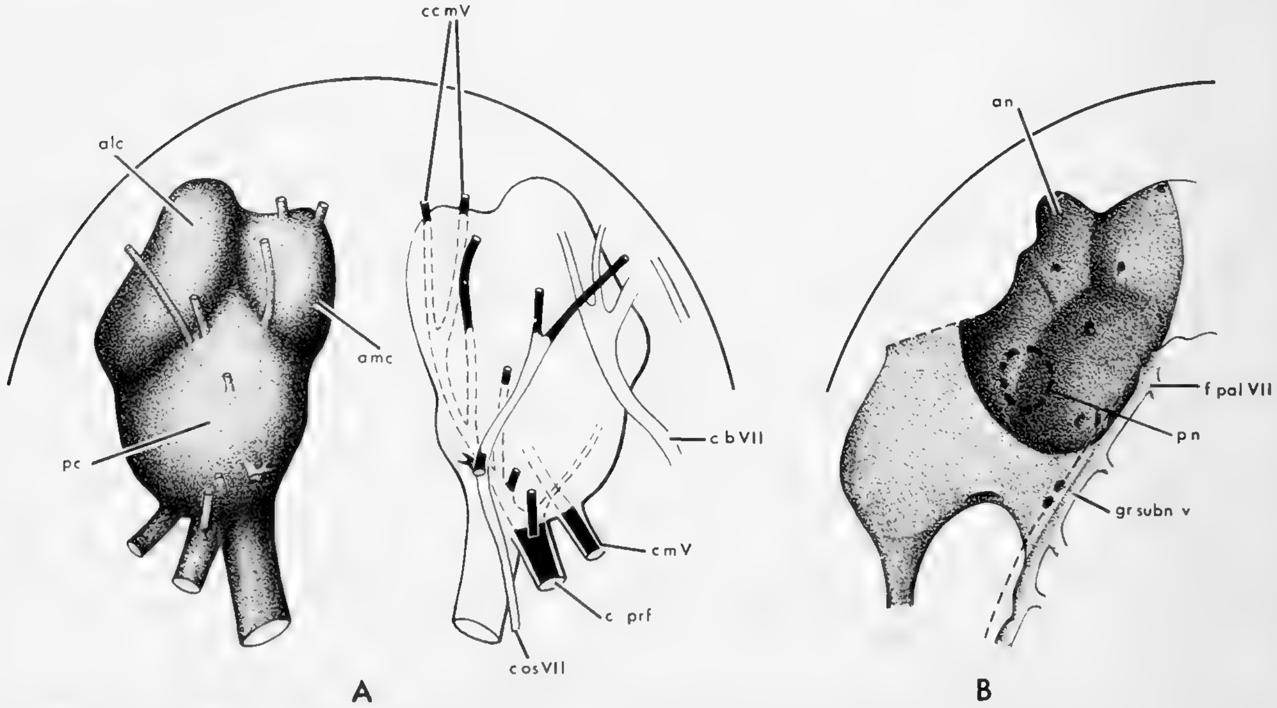


FIG. 29. *Dipnorhynchus sussmilchi*. Reconstructions of snout region. A) reconstruction of the nasal capsule. Left side of drawing shows the shape of the endocranial cavity; right side shows reconstruction of the canals passing through the endocranial cavity and tectum nasi. Portions of canals shown in black are represented by observed canals in specimens. B) nasal chamber in ventral view. Drawn with a portion of the anterolateral margin of the palate removed so as to reveal the groove for the subnasal vein.

of the anterior naris. There is also a small notch in the mid-line (Fig. 75), the significance of which is not clear but which is closely connected with the median internasal septum (p. 88). The position of the posterior naris is not clear. Immediately posterior and slightly lateral to the notch for the anterior naris there is a smaller slightly indistinct notch (Fig. 29B) on the margin of the lip. This does not seem large enough or posterior enough to have contained a narial structure. Immediately posterior to this there is preserved the anterior surface of a larger notch in the upper lip (Fig. 29B). This occurs in many other Dipnoi and such a posterior notch was earlier considered to have contained the posterior naris (see, e. g. Thomson, 1965). However, from the work of Jarvik (1964) on *Dipterus* it now appears that this notch marks the position of a small bony element supporting the fleshy portion of the upper lip. In view of the extremely close similarity between *Dipnorhynchus* and other Dipnoi in this respect (see also Denison, 1968a, b), it is necessary to conclude that the posterior naris was located in a posterior and more medial position, as is shown in Fig. 29B. (This problem is discussed further in our section entitled "Nasal Organ.")

The roof of the nasal capsule (tectum nasi) is thick but consists of extremely cancellous bone with a very thin perichondral layer. The dorsal, external surface is directly applied to the inner surface of the dermal skull roof. The inner surface of the tectum nasi bears three prominent rounded ridges which partially subdivide the nasal chamber into three portions—a principal posterior chamber, and smaller anteromedial and anterolateral chambers. A series of small canals for the passage of branches of the profundus V and opthalmicus VII nerves (possibly also ophthalmicus V) and also for blood vessels, pass through the tectum nasi opening at small foramina as shown in Fig. 29A. The passage of other small canals, including those opening at these foramina, is revealed by X-ray photographs. The patterns of the canals is shown in Figs. 29 and 30A. The main systems seem to be a series of branching canals, apparently stemming from one main canal, that pass forward in the tectum nasi and then pass ventrally through the tectum into the nasal cavity. These canals probably held the ophthalmicus superficialis VII nerve, which in modern Dipnoi has a similar distribution. Other canals (Fig. 29A) pass dorsally from the nasal chamber through the tectum nasi and these probably held branches of the fifth cranial nerve (Fig. 29A, *c prf*) as well as small blood vessels.

Apart from the small canals and foramina just mentioned, the tectum nasi is complete. Anteriorly and laterally the roof curves ventrally to form the anterior and lateral nasal walls. The anterior nasal wall is pierced by two prominent canals (Fig. 29A) which seem to have carried branches of the fifth nerve and vessels to the rostral tubuli. The lateral nasal wall is moulded around the dorsolateral margin of the anterior narial opening (Fig. 29B). The lateral wall is not continued ventrally to form a solum nasi and, in fact, if such a floor existed it must have been formed only in cartilage, for no trace of it is preserved in the fossils. The lateral nasal wall contains at least one longitudinal canal (as revealed by the X rays) which does not open into the nasal chamber directly and probably carried the r. buccalis VII forward from the orbital chamber (Fig. 29A). The nature of the narial openings will be discussed below ("Nasal Organ").

The internasal septum (septum nasi) is curiously developed. Between the posterior half of the nasal cavities it is dorsoventrally complete and fully separates the principal posterior nasal chambers of the cavities. Further anteriorly, however, the septum nasi is present only as a dorsal band of bone that curves upward as it passes forward and then, at the very tip of the nasal cavity, curves downward again to merge with the anterior nasal wall of each side. The anteromedial nasal chambers of each side are thus not completely separated by the bony septum nasi, although probably in life a ventral cartilaginous extension of the septum had this function. This is a problem of some importance in determining the homology of the nasal septum (see "Embryological Analysis"). As far as we can see no major foramina pierce the sides of the septum nasi.

Posteriorly the septum nasi is completely merged with the anterior portion of the braincase that overlies the palatoquadrate. The triangular tip of the palate projects forward to lie partly under the nasal chambers and presumably in life they were continuous with a cartilaginous solum nasi. Along the lateral margins of the tip of the palate on each side there is a large horizontal longitudinal groove (Fig. 29B, *gr subn v;* Fig. 78) passing backward under the nasal capsule into the orbital cavity. The dorsal rim of this groove was probably continuous with the solum nasi. This groove almost certainly carried a large vein backward from the nasal region toward the suborbital sinus, but there are also several canal openings that probably carried nerves into this groove. The most anterior of these may have served for the exit into the subnasal region of the palatal branch of the facial nerve (Fig. 29B, *f pal VII).*

The canal for the olfactory tract enters the nasal cavity in the posterior part of the internasal septum at a deep recess (Fig. 29A; Fig. 78) just medial to the proximal corner of the postnasal wall. The olfactory tract canal is divided into two portions by a vertical septum.

The principal bony portion of the postnasal wall is a stout ventral bar given off from the anterior portion of the endocranium at approximately the same level as the septum nasi. From a broad proximal base buttressed by the palate this bar extends almost directly laterally behind the nasal cavity. The distal end of the bar is developed into a broadly triangular flange. The anterior wing of this flange

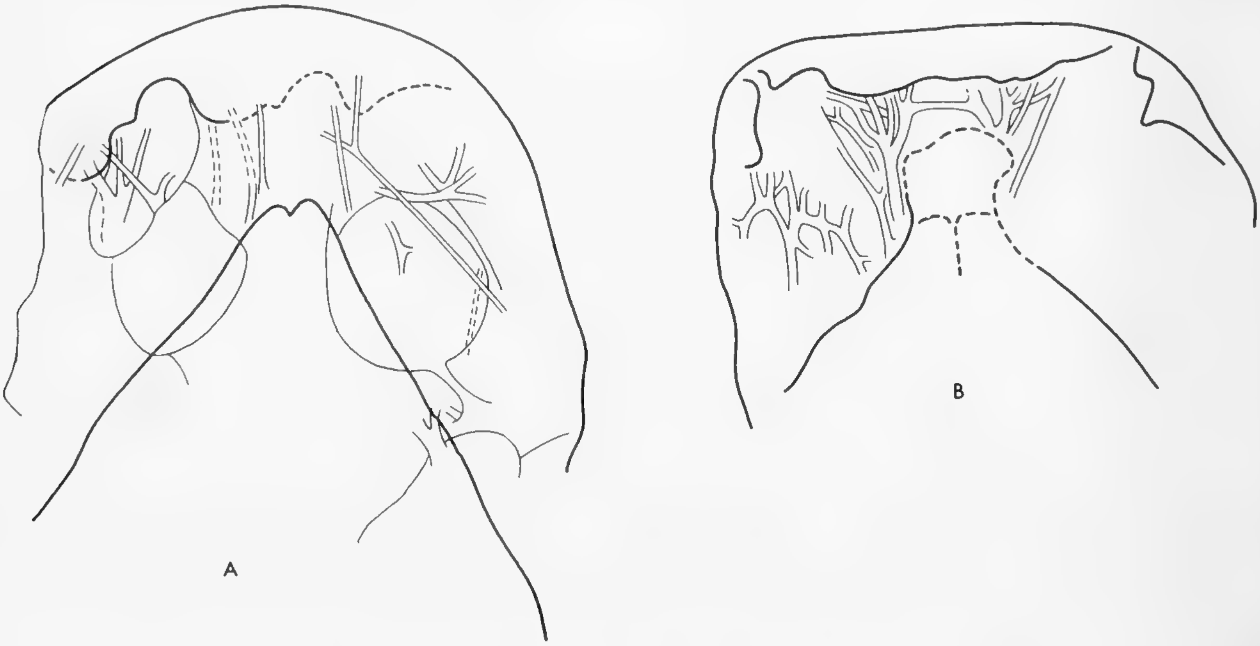


FIG. 30. Drawings showing the outlines of canal passing through the tectum nasi in: A) *Dipnorhynchus sussmilchi* (as shown by X-ray examination) and B) *Dipterus valenciennesi* (specimen 1859.33.612, Royal Scottish Museum).

(Fig. 29B; Figs. 74 and 75) merges with the lateral nasal wall to form the thick posterodorsal corner of the nasal capsule. The posterior wing of the flange reaches dorsally and posteriorly and forms a stout buttress under the inner surfaces of bones "O" of the dermal skull roof and the lateral margin of a deep recess extending forward from the orbital chamber. Dorsally the postnasal wall is continued as a thin lamina of bone that joins the posterior margin of the tectum nasi. This lamina is perforated by a large foramen for the profundus V nerve (Figs. 29A, *c prf).* In one specimen (18815) this profundus canal divides and two foramina—a large ventrolateral one and a small dorsomedial one—are found on the anterior surface of the postnasal wall. Apart from that for the profundus, the only canal to pierce the postnasal wall is fairly wide and opens posteriorly through the ventral surface of the distal part of the wall. This canal (Fig. 29A, *c m V)* is directed dorsomedially and enters the nasal cavity just lateral to the anterior opening of the profundus canal. Possibly it carried a r. maxillaris V or a portion of the profundus lateralis V.

ORBITAL REGION. Details of the external structure of the endocranium in the orbital region are revealed in specimen F 10813A; certain details of the passage of canals through the endocranial wall are revealed in the incomplete specimen P 33699, which has already been shown to indicate a great deal of the structure of the palatal region. From these specimens, and from X-ray photographs of specimen 18815, an almost complete picture has been built up of the structure in the orbital region (Figs. 31, 32). It lacks only detailed information concerning the shape of the endocranial cavity in this region.

The orbital region of the endocranium is here defined somewhat arbitrarily as the portion of the skull posterior to the postnasal wall and anterior to the transverse level of the lateral palatal process. The floor of the orbital chamber is formed

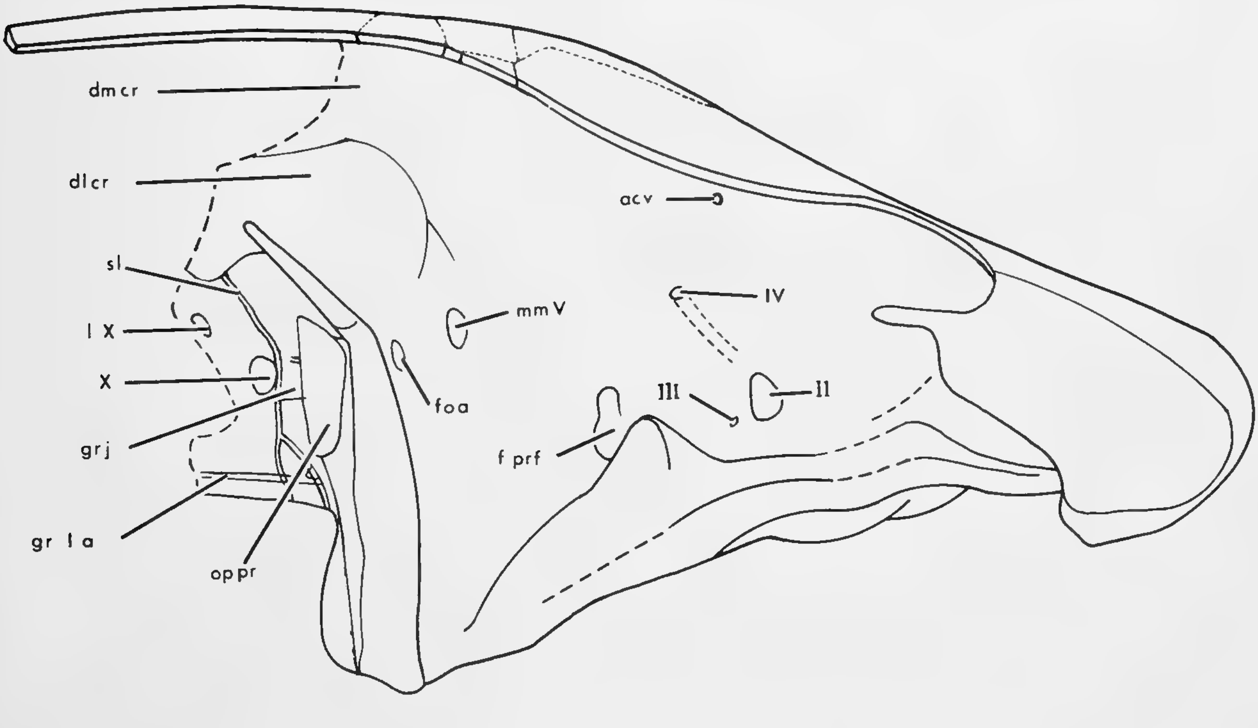


FIG. 31. *Dipnorhynchus sussmilchi.* Holotype. Outline drawing of braincase in right lateral view. Semidiagrammatic.

by the palatoquadrate. The medial wall of the orbital cavity is presumably almost entirely of neurocranial origin.

The following features mark the outer surface of the lateral wall of the braincase in the orbital region. Dorsally, in the deep pocket formed in the medial corner of the postnasal wall there is a foramen for the passage of the r. opthalmicus superficialis VII nerve (Fig. 32, *r os VII*) into the tectum nasi. Posterior to this foramen, just in front of the vertical level of the optic nerve foramen, there are two prominent triangular depressions in the lateral braincase wall. They are believed to be scars from the origin of eye muscles. The optic nerve foramen (Fig. 31; Fig. 78, 81) is large and set in the dorsal part of a depression which is formed by a second series of eye muscle scars. Immediately behind the lateral opening of the optic nerve canal there is a foramen for the third cranial nerve, which passes in a ventral direction through the lateral wall of the braincase before opening at the surface; above it is the foramen for the fourth nerve (Fig. 31, Fig. 73). Ventral and posterior to this foramen there is a laterally directed ridge, formed partly in the floor of the orbital chamber and enclosing the canal for the arteria ophthalmica magna (see above, "Palate"). High on the lateral surface of the endocranium behind the eye muscle scars, there is a foramen which possibly marks the exit of the anterior cerebral vein from the braincase (Fig. 31, acv; Fig. 78).

Even with the use of X-ray photographs, very little of the nature of the endocranial cavity in the orbital region could be determined. The principal distinguishable feature is the large dorsal canal extending upward toward the pineal openings on the skull roof (Fig. 32). It was also seen that the olfactory canals leading forward from the forebrain separate from each other at approximately the transverse level of bones O_1 of the skull roof.

TEMPORAL AND OTIC REGIONS. The temporal and otic regions are here considered together for convenience in discussing the passage of various canals (e. g., for the lateral head vein, hyomandibular nerve, etc.) that pass between the orbitotemporal chamber and the posterolateral face of the otic region.

The temporal region may be considered as bounded anteriorly by the ridge in the floor of the orbital chamber, through which the a. ophthalmica magna passes, and the lateral palatal process. Like the orbital chamber the temporal chamber is roughly triangular in cross section. The palatoquadrate forms its floor, and the neurocranial wall to which parts of the palatoquadrate have become fused (see "Embryological Analysis") forms the medial wall. Posteriorly the great lateral "wings" of the endocranium extend laterally to form the curving posterior wall of the temporal chamber, enclosing the otic capsule in front, and forming a massive buttress for the quadrate-mandibular articulation. This heavy wing of the endocranium is a solid structure and presumably represents the fusion of a processus oticus palatoquadrati with the median neurocranial wall and a massive processus basitrabecularis. The dorsolateral margin becomes narrower and is applied to the undersurface of bone Y_1 or the Y_1–Y_2 contact of the skull roof (Fig. 81). The articular surface (Fig. 77) of the quadrate is not preserved. There is a roughly triangular concave area where the perichondral layer is missing and where we presume that, as on the articular bone of the mandible, there was in life a cartilaginous pad.

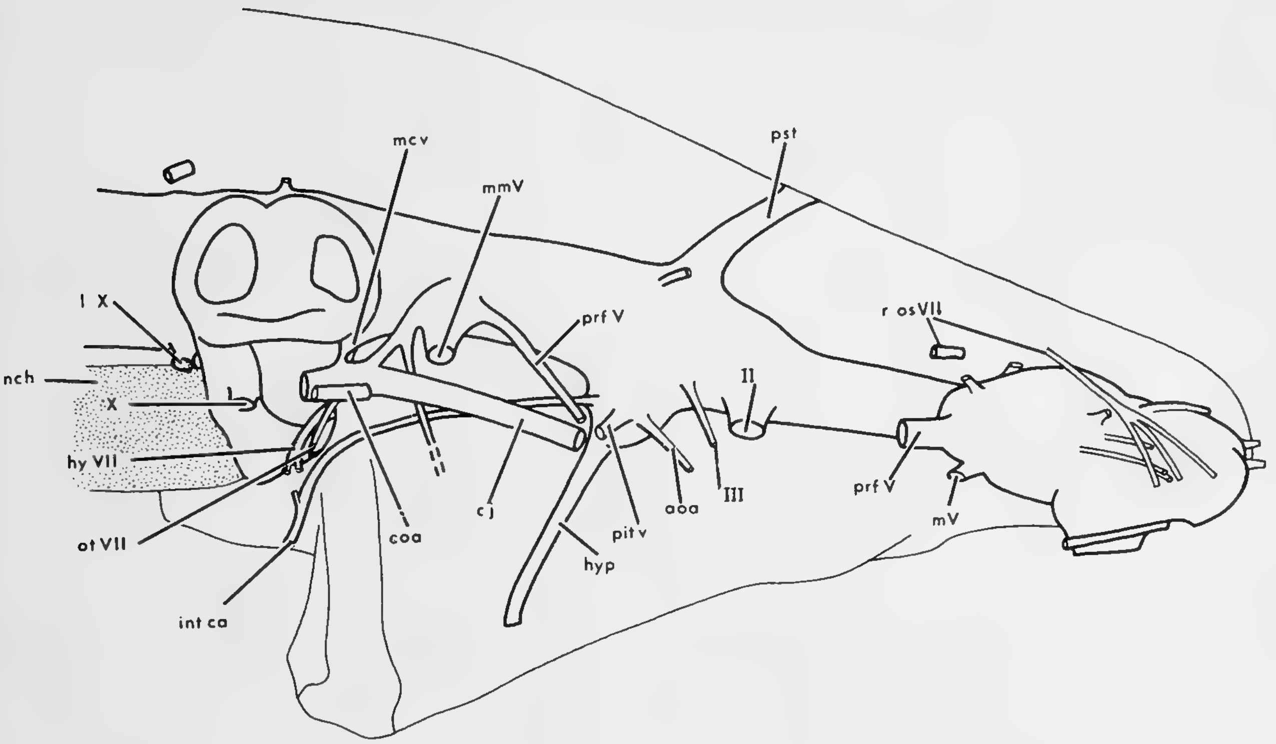


Fig. 32. *Dipnorhynchus sussmilchi*. Reconstruction of the endocranial and notochordal cavities in right lateral view.

The floor of the temporal chamber is an essentially single, smooth surface, marked only by a ridge curving from the tip of the lateral palatal process to the quadrate (Fig. 73). This ridge separates the concave floor of the chamber from a convex anterolateral surface that is a posterior continuation from the orbital region. The anteromedial wall and the ventral part of the posterior wall of the temporal chamber are almost vertical, but the posterior wall is continued posteromedially completely over the whole otic region under dermal bones J and I, giving a very large surface for the origin and enclosure of the temporal musculature. This large posterior chamber is subdivided into two portions on each side by a prominent ridge, the dorsolateral crista, that passes posteriorly and slightly medially, becoming progressively taller until it reaches the undersurface of the dermal skull roof at bone I and the posterior part of bone J. This dorsolateral crista separates a medial recess for the temporalis muscle from a more lateral recess for the masseter muscles. The two medial recesses are separated in the midline by a very thin lamina of bone suspending the endocranium from the underside of the skull roof (Fig. 76). As this dorsal lamina is traced forward, it bifurcates as it comes to contain the parietal stalk passing dorsally from the endocranial cavity.

Anteriorly, slightly behind the level of the lateral palatal process, the median wall of the temporal chamber is pierced by a large anteriorly directed recess marking the opening of the larger jugular canal (Fig. 31, *f prf*). Within it is a small dorsal foramen, which marks the emergence of the profundus nerve canal into the main canal for the jugular vein. Through the medial wall of the recess into which these foramina open is a smaller foramen for the pituitary vein. Directly in front of the anterior limit of the dorsolateral crista is a large foramen (Figs. 78, 81) through which passed the maxillary and mandibular branches of the trigeminal nerve and probably also the ramus ophthalmicus superficialis of the facial nerve.

Immediately lateral to this, facing directly forward, is the foramen for the orbital (stapedial) artery (Fig. 31). The internal connections of these various foramina are discussed below.

As we have already noted, the otic capsule itself is largely obscured by the massive development of the lateral wings of the braincase. The posterior face of the lateral wing of the braincase is very interesting because we may here clearly distinguish, in addition to the neurocranial and palatal elements, a further element that has also become partially fused into this complex (Fig. 31; Figs. 82, 83, 84). This structure is a stout bar of bone that reaches laterally and ventrally across the posterior face of the palatoquadrate. Proximally it is divided and encloses the posterior opening of the jugular canal. It extends laterally as a massive bar, marked by grooves for blood vessels (see below), to a lateral articular facet right at the end of the skull (Fig. 83). This seems to be a facet for the articulation of the operculum. Ventrally, the main portion of the structure continues to the region of the quadrate articulation. The whole structure is separated from the palatoquadrate (except along its dorsal edge) by a deep recess (Fig. 83) that can only be interpreted as a blind spiracular recess having contained a spiracular sense organ (see "Soft Anatomy"). A separate, very narrow, cleft separates the tip of the "opercular process" from the wing of the palatoquadrate. It is tempting to interpret this whole structure as a hyomandibula that has become fused to the palatoquadrate as a structural brace. It has the basic features of a crossopterygian hyomandibula—a double proximal head around the jugular vein, an opercular process and quadrate process (and presumably also a connection, unpreserved, to the ceratohyal). An alternative explanation is that this structure is not a hyomandibula but a massively expanded part of the lateral braincase wall of a type not otherwise seen in fishes and onto which a separate hyomandibula was articulated. However, the facet interpreted here as serving for opercular articulation seems too far lateral in position to receive a hyomandibula. There seems to be no way of resolving these difficulties of interpretation at present. The materials from the Australian Gogo Fauna currently being studied by Drs. Miles and Andrews in Great Britain, may elucidate the problem further.

For the present we will refer to this structure as the "otoquadrate bar."

Running diagonally anteroventrally across the wall of the otic capsule is a narrow ridge enclosing a canal, possibly vascular in origin. Under the projecting wall of the otic capsule is a wide horizontal groove which is the posterior continuation of the jugular foramen and clearly served for the passage of the jugular vein (Fig. 31). A curving ridge on the otoquadrate bar, ventral to the jugular foramen, defines the passage of the orbital artery into the jugular foramen. A second, horizontal ridge on the posterior face of the "opercular process" defines the position of the first efferent arterial arch (Fig. 83). The area immediately ventral to this second ridge seems also to be a region of muscle insertion. The ventrolateral process of the otoquadrate bar is marked by a deep groove for the ramus mandibularis externus VII nerve, running from the spiracular cleft under the otoquadrate bar (Fig. 83).

Within the spiracular cleft are openings for the r. hyomandibularis VII and r. oticus VII nerves. A groove for the ramus mentalis internus VII nerve passes along the posterior face of the lateral wing of the braincase after dividing from the groove for the r. mandibularis externus VII (Fig. 31; Fig. 38).

Further posteriorly, a prominent feature of the otic region is the foramen for the tenth cranial nerve, in the posterior part of the jugular groove (Fig. 32). Immediately ventral to the tenth nerve foramen is a smaller foramen of unknown origin opening into an anterodorsally directed groove. The groove for the orbital artery may be traced ventrally from the jugular foramen towards the groove for the lateral aorta (Fig. 32). Ventrally, the broad base of the otic region between the clefts for the spiracular organs shows a paired structure (Fig. 75). The basal region on each side seems to be continuous with the posterior face of the lateral wing of the endocranium. The only prominent features of this basal region are the presence of a small foramen in the most ventral part of the lateral wall that is connected posteriorly with a groove passing along the ventral surface of the occipital region. The groove (Fig. 31) is interpreted as having carried the lateral aorta, and the foramen as marking the position of entry of the internal carotid artery into the endocranium. Just behind this foramen the groove for the orbital artery curves upward, over the lateral wall of the braincase. One may guess from the arrangement of the otic region that the recesses for the temporalis muscles, between the dorsal and dorsolateral cristae, extended posteriorly over the occipital region under bones A and H of the skull roof. However, the cristae themselves only extended as far backward as the undersurface of bone I. The recess for the masseter muscle, lateral to the dorsolateral crista, terminated over the otic capsule. Since there is no separate region for the insertion of the axial musculature reaching forward from the trunk one must presume that it occupied the posterior part of the "temporalis" recess. Having described the general external features of the temporal and otic region, we may now describe the internal structure. The general shape of the endocranial cavity is shown in Figure 32.

The cavity for the inner ear organ in *Dipnorhynchus sussmilchi* is widely confluent with the general neurocranial cavity. The anterior vertical semicircular canal is distinct and lies within the dorsolateral crista of the otic region. The posterior semicircular canal runs in the posterodorsal margin of the otic capsule; the ridge enclosing it forms the posterior limit of the masseter muscle chamber. The horizontal canal lies just beneath the surface of the otic capsule between the maxillary-mandibular foramen anteromedially and the jugular canal laterally. A vertical septum arising from the posterior wall of the labyrinth cavity separates an anteromedial cavity for the recessus utriculi from a medial recessus sacculi. The latter is confluent medially with the general neurocranial cavity, but is also continued dorsally as the cavity for the crus communis. Anteriorly the lateral wall of the endocranial cavity medial to the trigeminofacialis ganglia is marked by a prominent groove that turns into the anterior portion of the recessus utriculi and then passes out laterally into a canal piercing the lateral wall of the otic capsule and merging into the medial portion of the jugular canal. This is the canal for the vena cerebralis medialis (Fig. 32, *mcv*). No clear indication of the passage of the acoustic nerve is recorded on the bony wall of the capsule. Presumably it left the brain at a point somewhat posterior to the vena cerebralis medialis and passed directly toward the labyrinth organ without touching the bony capsule wall. The floor of the neurocranial cavity is not preserved in the otic region and presumably was a very thin lamina of bone separating the neurocranial cavity from the rapidly tapering notochordal canal (Fig. 32). Anteriorly, at the level of the trigeminofacialis ganglion complex, the floor of the neurocranial cavity bears a prominent long median ridge that may indicate that the myelencephalon in this region had a paired shape. This is most unusual and has not been recorded in other Dipnoi. The notochordal canal, which is wide in the occipital region and the posterior part of the otic region, tapers extremely sharply anteriorly so that it terminates at the level of the midpoint of the recessus sacculi (Fig. 32, *nch).*

The arrangement of the cranial nerves and of certain major blood vessels is largely revealed through study of two important regions: the hypophysial recess and the region of the trigeminofacialis ganglion complex and jugular canal.

The hypophysial recess is best seen in specimen P 33699 (Figs. 26 and 32). A large recess is present, from which an extremely narrow hypophysial canal leads ventrally to the hypophysial opening in the palate (Figs. 26, 32, *hyp;* Figs. 74–75). Leading out of the recess on each side are three major canals. The posterior one (Fig. 32, *int ca*) may be traced backward into the occipital region; it is the canal for the internal carotid artery. This leads through the base of the otic and temporal region, very briefly enters the jugular canal near its connection with the profundus canal, and then bends medially to enter the hypophysial recess. The middle canal opening into the hypophysial recess on each side leads directly laterally and opens into the anterodorsal portion of the recess at which the combined profundus-jugular canal opens into the temporal chamber. This is the canal for the pituitary vein (Fig. 26, *c pit v*). The anterior canal passes anterolaterally to open into the palate just lateral of the optic nerve foramen. This is the previously mentioned canal for the arteria ophthalmica magna which presumably branches from the internal carotid artery within the hypophysial recess.

The jugular vein (or lateral head vein) runs posteriorly through the otic region in a wide canal, the anterior opening of which is in the temporal chamber and also serves for the exit of the profundus V nerve into the temporal region. It opens posteriorly at the jugular foramen as previously discussed. The orbital artery also passes into the jugular foramen and then branches off and opens anteriorly through a separate canal and foramen (Fig. 31, *f o a)* into the temporal chamber.

The trigeminal and facialis cranial nerve ganglia lie in a pocket formed within the lateral wall of the braincase. Presumably the outer wall of the pocket is formed by the processus ascendens palatoquadrati; the medial wall is endocranial. The pocket opens anteriorly into the endocranial cavity and nerve rami emerge from the pocket through three separate canals. An anterior canal (Fig. 32) carried the profundus V to its anterior opening into the jugular canal. A large laterally directed canal carried the r. maxillaris V and r. mandibularis V to an exit foramen in the temporal chamber. A third canal leads posteroventrally and seems to have carried the r. hyomandibularis VII. Immediately after the emergence of this canal from the trigeminofacialis chamber, a smaller canal divides off from the palatal region. This canal (Fig. 32) carried the r. palatinus VII. The canal for the r. hyomandibularis VII passes into the jugular canal. Apparently the nerve ramus ran across the canal and then passed ventrally into the tip of the spiracular cleft (Fig. 32). A second short canal (Fig. 32) carried the r. oticus VII which proximally must have run into the hyomandibular canal. There is no sign of a separate canal for the passage of the r. ophthalmicus superficialis VII; it seems most probable that this nerve emerged from the braincase through the maxillary-mandibular V foramen.

Occipital Region. Only one of the available specimens (F 10813A) shows any part of the occiput; in it only the anteroventral region and a small portion of the lateral wall are preserved (Figs. 75, 77; Figs. 78, 81; Figs. 82-84). A most interesting feature of the occiput is the presence, on each side of the specimen, of a sulcus passing behind the otic capsule through the anterior margin of the tenth cranial nerve foramen and ventrally behind the root of the otoquadrate bar to meet its fellow of the other side. It is tempting to regard this sulcus (Fig. 31, *sl;* Fig. 78) as representing the separation between the otic and occipital regions of the skull; for the purposes of description, this hypothesis will be followed here. The possible homology of this sulcus is considered further.

A second foramen for the tenth cranial nerve (possibly a superior lateralis ramus) is located midway up the lateral neurocranial wall, tucked under the posterior corner of the otic capsule. Just below this foramen is a vertical canal carrying the occipital artery into the endocranial cavity. Behind this point, the lateral braincase wall is extremely thin and delicate; only the ventral portion is more solid. On either side of the ventral occipital region, the wall of the neurocranium is continuous with that of the otic region and bears the posterior part of the groove marking the passage of lateral dorsal aorta. Ventrally, the lateral wall curves medially (Fig. 83) and then it passes dorsally again in the form of a delicate vertical lamina just lateral of the midline. The laminae from each side join in the midline, forming a narrow medial cleft in the ventral surface of the occiput (Fig. 84). In the midline itself there is a median vertical septum extending further dorsally from this point into the cavity for the notochord. The notochordal canal tapers sharply as it passes toward the otic region. Although it is imperfectly preserved in our material, there is an indication of an horizontal septum separating the canals for the notochord and brain-stem. It has not been possible to see if this horizontal septum meets the vertical septum that seems to divide the notochordal canal. The significance of the vertical septum and the medial cleft on the ventral surface of the occiput is not known. Presumably the paired structure forming the ventrolateral walls of the occiput and enclosing the median cleft between them is formed by the parachordals.

COMPARISON WITH OTHER PALEOZOIC DIPNOI

Dipnorhynchus lehmanni. We have studied the descriptions of *D. lehmanni* by Westoll (*in* Lehmann and Westoll, 1952) and Lehmann (1956) and the interpretations of these forms by Jarvik (1954). However, we are forced to conclude that many of the features identified in these accounts are so imperfectly defined on the specimen that their identity is uncertain at best. The following features may be compared with reasonable confidence. The anterior pterygoids ("vomers") are overlapped by the anterior portion of the palate; this is not seen in *Dipnorhynchus sussmilchi* but is seen in *Uranolophus* (below). The dental structure is different, with the presence of more definitely shaped subconical tubercles having the appearance of being arranged in three "radiating" rows. However, this pattern of lateral tubercles could presumably be derived by a relatively minor modification of the pattern in *D. sussmilchi.*

In the description of *D. lehmanni* the composition of the palate is far from clear. Westoll (*in* Lehmann and Westoll, 1952) has figured the palate with separate pterygoid and parasphenoid elements and also identified basipterygoid processes. He considers the structure clear enough to be "strong support" for the view that early Dipnoi had a kinetic skull with a divided endocranium as in Crossopterygii. Jarvik (1954) gives a sketch and photograph of a cast of the palate of *D. lehmanni.* He does not show any separation between parasphenoid and pterygoid nor does he identify the basipterygoid processes. We are inclined to accept this part of Jarvik's description and, since the skull of *D. lehmanni* is completely crushed, we consider it most probable that the ridges in the palate identified as the parasphenoid and basipterygoid processes are actually caused by the crushing of the palate into the endocranium. This does not mean that the parasphenoid is absent in *D. lehmanni,* but the available evidence seems to suggest that the palate in this form, as in other Dipnoi, is fused to the undersurface of the endocranium and shows no sign of kinetism. Jarvik (1954, figs. 36A, 37A) has also described in his casts of *D. lehmanni* a posterior projection from the palate, which he interprets as a posterior parasphenoid stalk comparable to that found in Middle Devonian and younger dipnoans. The accounts of Westoll and Lehmann give no sign of such a structure. It could equally well be an indication of the posterior part of the braincase (the ventral surface of which, as we have previously seen, is paired in *D. sussmilchi*). It is also not impossible that it is an artifact (see Lehmann *in* Lehmann and Westoll, 1952, for an account of difficulties encountered in preparing the material).

Until the details of the palate in *D. lehmanni* are more fully understood we continue to include it in the genus *Dipnorhynchus,* but with some reservations (see also discussion by Denison, 1968a).

Uranolophus. The otherwise rather well-preserved material of the oldest known dipnoan *Uranolophus wyomingensis,* as described by Denison (1968a, b), unfortunately does not reveal any details of the structure of the braincase except that both perichondral and endochondral ossifications were present. However, it is possible to make some useful comparative observations on the palate of *Uranolophus.*

The ventral aspect of the palate in the nasal region (Denison, 1968a, fig. 8) shows an arrangement of the nasal organ generally similar to that of *Dipnorhynchus,* or indeed most other fossil dipnoans. There is a prominent notch for the anterior naris; the posterior naris must have been located in the most posterior part of the capsule as Denison notes. It seems most probable that the solum nasi was present only in cartilage as in other forms. The median internasal septum is approximately as wide as in *Dipnorhynchus,* but no details of subdivision of the nasal chamber may be seen. The nasal capsule is relatively shorter than in *Dipnorhynchus.* The ventral bar of the postnasal wall is developed exactly as in *Dipnorhynchus.* In the palate there are separate vomers, pterygoids, and a median parasphenoid. The anterior pterygoids ("vomers") are more or less the same as in *Dipnorhynchus,* but there is no space between them and the pterygoids. Denison suggests that they were overlapped by the anterior margins of the pterygoids. As in *Dipnorhynchus* they partially underlie the nasal capsule. The parasphenoid is extremely broad in

Uranolophus and extends far forward between the pterygoids but has no posterior stem. In this last feature *Uranolophus* and *Dipnorhynchus* differ importantly from the later Dipnoi. There is no external hypophysial opening. The dermal bones of the palate in *Uranolophus* lack well-developed tooth plates, such as seen in later forms, but are covered with small denticles. Laterally a ridge on the side of the pterygoids forms the only modification of the essentially flat occlusal surface. This is also clearly a major point of difference from *Dipnorhynchus* and other known dipnoans.

As in *Dipnorhynchus,* the dorsal surface of the palate in *Uranolophus* is thickened to buttress the braincase underneath the postnasal wall and just in front of the optic nerve foramen. Also present in *Uranolophus,* but in no other known dipnoan except *Dipnorhynchus,* is the conical "lateral palatal process" which Denison (1968a) believed to be an additional point of support of the pterygoid but, as far as we can determine, does not attach to any other structure in either genus. The vascular and nervous system associated with the palate in *Uranolophus* cannot be fully identified, but the foramen for the arteria ophthalmica magna is seen in the floor of the orbital chamber, in the same position as in *Dipnorhynchus.* There is also an indication of the marked lateral groove passing around the margin of the anterior part of the palate under the postnasal wall, that is considered to have held a subnasal vein in *Dipnorhynchus* (see also *Ganorhynchus,* below). The overall similarity between *Dipnorhynchus* and *Uranolophus* with respect to the dorsal surface of the palate strongly suggests that the adductor muscle system and temporal chamber were essentially the same in the two genera.

Dipterus. Unfortunately, the amount of information that we have concerning the endocranium of the Middle Old Red Sandstone dipnoan *Dipterus* is very small in comparison with the extensive and finely detailed information that we have concerning the dermal bones of the skull roof. Woodward (1891), Goodrich (1909) Watson and Day (1916) Säve-Söderbergh (1952), Jarvik (1954, 1964), and Gross (1964) have provided partial information and restorations, but only White (1965) has been able to study material of the whole endocranium. White's specimen was incomplete in the nasal region, but we are able to describe here some details of the structure of this region from a study of a specimen from the Royal Scottish Museum (RSM 1859–33–612 *Dipterus valenciennesi*). From this new material and from Jarvik's study of the narial opening and upper lips, we are able to make a reasonably complete restoration of the anterior portion of the endocranium of this fish. Although Jarvik (1964) was able to describe the details of the narial openings in *Dipterus,* so far as we know, only one specimen exists that shows internal endocranial details in the rostral region. In this specimen the perichondral-bone lining of the dorsal surface of the nasal capsules has been eroded away, exposing the internal network of ramifying nerve and vascular canals (Fig. 30B, Fig. 68).

In most principal features the endocranium of *Dipterus* is similar to that of *Dipnorhynchus.* There are, however, significant differences between the two. The process behind the notch for the anterior naris (Fig. 30) is much smaller in *Dipterus,* and in other dipnoans (see p. 71) than in *Dipnorhynchus.* This is probably associated with the relatively larger extent of the nasal capsule in *Dipnorhynchus* than in later genera and may be connected with the development of a cartilaginous subnasal septum, extending medially between the two nares. The composition of the postnasal wall is shown best in White's account of *D. valenciennesi* (1965, figs. 43, 44). It is buttressed by a large process from the palate exactly as in *Dipnorhynchus* (although rather more strongly developed). It is not possible to distinguish an orbitonasal groove under the postnasal wall in *Dipterus.*

From White's description it is clear that in dorsal aspect the overall shape of the endocranium in *Dipterus* is generally similar to that of *Dipnorhynchus.* The dorsal margin of the lateral wing of the palatoquadrate is attached to the undersurface of the same dermal skull roof elements as in *Dipnorhynchus.* However, there may be differences in the otic and occipital regions. In White's specimen (P 17410) the simple medial dorsal septum that in *Dipnorhynchus* separates the chambers for the temporalis musculature of either side is not present. The skull of this specimen is relatively much lower and the temporalis chambers are separated by the neurocranium, which is applied directly to the undersurface of the skull roof itself. The neurocranium is wide in this region and contains a large cavity interpreted by White as containing a diverticulum of the endolymphatic duct. The chambers for the masseter and temporalis musculature are small in the otic region. Although the neurocranium is largely missing in the specimen of *Dipterus* mentioned previously in connection with the rostral anatomy, there is a definite indication on the underside of the dermal skull roof of both the dorsolateral cristae and a median crista. These are arranged as in *Dipnorhynchus* and are shown in Figure 68. The possibility therefore exists that in *Dipterus* there was a very low dorsomedian crista that has been crushed in specimen P 17410.

In lateral and ventral aspects, further important differences between *Dipterus* and *Dipnorhynchus* are seen. In *Dipnorhynchus* the quadrate articulation is located at the level of the center of the otic capsule and the posterior face of the temporalis chamber is essentially a vertical lamina. In *Dipterus* the posterior wall is inclined at an angle of approximately 45°, carrying the quadrate articulation forward to approximately the level of the profundus foramen. As a consequence, the cheek region is greatly reduced anteroposteriorly in *Dipterus.* The opercular chamber is modified accordingly, and we may note that the efferent pseudobranchial artery in *Dipterus* comes for part of its course to lie in a canal enclosed within the lateral palatoquadrate wing. There seems to be no lateral palatal process in *Dipterus.*

As far as may be discerned, the arrangement of the cranial nerve and vascular foramina in this orbitotemporal region of *Dipterus* is identical with that of *Dipnorhynchus* with only slight differences in position. On the posterior face of the palatoquadrate, however, there are important differences. The jugular vein passes backward through a jugular canal and then posteriorly in a groove on the lateral otic wall, but the hyomandibular nerve in *Dipterus* apparently left the endocranium through a foramen directly lateral to the posterior jugular foramen, and the orbital artery passed into the braincase at a point considerably ventral to these two foramina. No sign of a separate hyomandibular is present and one can only conclude that no hyomandibular structures have become incorporated into the braincase in any recognizable manner. If a hyomandibular had simply been fused into the posterior face of the palate, presumably the orbital artery would have continued to pass over it dorsally, as is the case in *Neoceratodus.* The only way in which one could satisfactorily accommodate the hyomandibular into the otic region would be if the canals for the orbital artery and hyomandibular nerve had been misinterpreted and were in fact reversed. However, their appearances in White's figures (1965, figs. 43, 46) belies this; furthermore, there is good corroborative evidence from the structure of another Devonian form, *Chirodipterus,* that White's identification of the hyomandibular nerve foramen is correct.

In ventral aspect also the endocranium of *Dipterus* differs in important features from that of *Dipnorhynchus.* The palatoquadrates and pterygoids in *Dipterus* are widely separated posteriorly from a point in front of the hypophysial opening. The latter is located far in advance of its position in *Dipnorhynchus* and lies in the anterior part of a large rhombic parasphenoid that extends posteriorly under the otic region. This is also a product of the proportional changes by which the quadrate articulation is brought forward, leaving a considerable ventral surface behind the palate.

Ganorhynchus. In 1965, Gross described certain features of the anatomy of the rostral region in the upper Middle Devonian dipnoan *Ganorhynchus splendens* Gross. In many ways there is considerable resemblance between the structures seen in the nasal region of this form and that of *Dipnorhynchus sussmilchi.* The nasal cavity in *Ganorhynchus* is partially subdivided into three portions that correspond exactly to the anteromedial, anterolateral and posterior recesses of *Dipnorhynchus.* The arrangement of the small canals piercing the tectum nasi in *G. splendens* is rather different from that of *D. sussmilchi.*

The postnasal wall in *G. splendens* is pierced by two important canals. The first is easily homologized with the profundus canal of *D. sussmilchi.* The second is a canal of varying manifestation termed the orbitonasal canal by Gross and homologized with the similarly named canal in *Chirodipterus* (see below). On the left side of Gross' specimen this canal passes ventrally and medially of the profundus canal to emerge into the ventromedial corner of the nasal cavity and passes along the lateral side of the palate in a elongate groove. On the right side of Gross' specimen (wrongly labelled in his figure 1, 1965; personal communication) the relative positions of the profundus and orbitonasal canals are different. The profundus is situated slightly medially of the orbitonasal canal, but the latter nonetheless leads anteriorly into a groove along the side of the tip of the palate. In *Ganorhynchus,* exactly as in *D. sussmilchi,* two canals on each side lead directly forward from the anteromedial recess into the region which in *Dipnorhynchus* is occupied by the rostral tubuli. Also, as in *Dipnorhynchus,* the internal septum is more complete posteriorly, and anteriorly it is present only as a dorsal band. In *Ganorhynchus* the canals for the olfactory tracts merge together at the level of the postnasal walls, while in *D. sussmilchi* they fuse somewhat further posteriorly. In *Ganorhynchus* the palatal dentition extends anteriorly underneath the septum nasi, considerably further than in *Chirodipterus* and approximately to the same extent as in *Dipnorhynchus.* It seems possible, therefore, that the sharply pointed tip of the palatal dental battery includes a pair of "anterior pterygoid" elements similar to those of *Dipnorhynchus.*

Chirodipterus wildungensis. The first full description of the endocranial anatomy of a fossil lungfish was given by Säve-Söderbergh (1952) in a beautifully detailed account of the lower Upper Devonian genus *Chirodipterus* from Wildungen in Germany.

In many features the anatomy of *Dipnorhynchus* is remarkably similar to that of *Chirodipterus.* Several of the features in which the two differ demonstrate clearly the more primitive nature of *Dipnorhynchus* and aid our interpretations of the later forms.

Whereas the ethmoidal region in *Dipnorhynchus* is somewhat flattened in transverse section, that of *Chirodipterus* is strongly rounded. The arrangement of the "lips" around the dorsolateral surface of the endocranium is remarkably similar in the two genera. From the new information that is available concerning the position of the narial openings in *Dipnorhynchus* and *Dipterus* we may see that the posterior naris in *Chirodipterus* must have had a similar position. The notch in the lateral margin of the snout that lies immediately behind the notch from the anterior naris did not house the posterior naris, as previously suggested (Thomson, 1965), but rather the small element supporting the upper lip (see especially Jarvik, 1964). As in other known forms, there is no sign of a ventral wall to the nasal capsule in *Chirodipterus.* The internasal septum is similar to that of *Dipnorhynchus* being complete dorsoventrally only in the posterior portion of the nasal region. The deep recess from the posterior corner of the nasal cavity into which the olfactory tract opens in *Dipnorhynchus* is not developed in *Chirodipterus* (see Säve-Söderbergh, 1952, fig. 3); there seems no indication of any subdivision of the nasal cavity into the three recesses seen in *Dipnorhynchus.* Few canals or foramina in the dorsal nasal roof are illustrated by Säve-Söderbergh, but an interesting feature is the presence of two major canals in the postnasal wall. The first of these is readily identified as the profundus canal, which seems to divide within the postnasal wall and emerge into the cavity by three separate foramina. The second canal is an enigmatic structure that Säve-Söderbergh termed the orbitonasal canal. It apparently connects three separate foramina in the posterior face of the postnasal wall to a single internal foramen in the medial corner of the nasal cavity where it leads into a groove passing around the medial surface onto the side of the septum nasi. The significance of this structure (which is also seen in *Ganorhynchus,* see p. 83) is difficult to determine. However, it seems unlikely that it contained any nerve. The groove on the posterior medial corner of the nasal cavity into which the orbitonasal canal passes, however, is remarkably similar to the lateral subnasal groove on the side of the palate in *Dipnorhynchus.* This resemblance is even more marked in the specimen of *Ganorhynchus* described by Gross (1965). In *Dipnorhynchus* this groove seems clearly to have carried elements of the venous system backward from the nasal region to the suborbital sinus. Under the postnasal wall it receives several small veins from the palate and also (Fig. 29) from the postnasal wall itself. It seems possible that the orbitonasal canal of *Chirodipterus* and *Ganorhynchus* also carried veins backward from the nasal region. In this case it would be necessary to explain why the canal turns to enter the postnasal wall instead of continuing beneath it as in *Dipnorhynchus.* This may be partly explained by an increased development of the palatal buttress under the postnasal wall in the younger forms so that there is less space beneath it. It may also be significant that the canal for the ramus maxillaris V in *Dipnorhynchus* is widely separated from the vascular groove discussed above, while in *Chirodipterus* it is associated extremely closely with the orbitonasal canal and in *Ganorhynchus* the orbitonasal canal is undivided and the canal for the r. maxillaris V does not seem to be present. Possibly the orbitonasal canal of *Chirodipterus* and *Ganorhynchus* represents a passageway for veins leading from the nasal region to the suborbital sinus, perhaps running in conjunction or close association with the maxillaris V nerve.

In the general composition of the orbitotemporal region there is remarkable agreement between the structure of *Dipnorhynchus* and *Chirodipterus,* with an identical arrangement of the optic, third and fourth nerves, the canal and foramen for the ophthalmica magna artery, the pituitary vein, profundus-jugular canal foramen, trigeminal nerve foramen and orbital artery. Internally the composition of the trigeminofacialis ganglion recess is different, in that the vena cerebralis medialis is closely associated with the seventh cranial nerve (r. hyomandibularis), while in *Dipnorhynchus* this vein seems to enter the jugular canal separately and somewhat posteriorly. The jugular canal has the same relationship to the trigeminofacialis ganglia and nerves. The canal for the ramus palatinus VII in *Chirodipterus* apparently also enters the jugular canal for a short distance. The anterior face of the lateral wing of the braincase stands at an angle of about 75°, compared with 90° in *Dipnorhynchus* and 45° in *Dipterus.*

The arrangement of the dorsomedian and dorsolateral cristae is the same in the two genera, as is the general structure of the inner ear.

An important difference between *Dipnorhynchus* and *Chirodipterus* is to be found in the structure of the posterior face of the palatoquadrate. In *Chirodipterus* the massive otoquadrate structure seen in the former genus is absent. However, it is interesting that in this form the posterior openings of the canals for the jugular vein and the orbital artery are separate, while they are connected briefly internally where the hyomandibular nerve apparently transfers its course from one canal to the other. This is what one would expect to be the situation if the hyomandibular had been lost from the endocranium. If the hyomandibular were simply incorporated into the endocranium one might expect to see a common external posterior foramen for the jugular vein and orbital artery. Furthermore, there seems to be no sign in *Chirodipterus* of a spiracular cleft.

The internal carotid artery in *Chirodipterus* passes forward externally to the braincase, only entering it just behind the hypophysial foramen, the latter being relatively anterior in position. This is in accordance with the relatively weaker development of the palatoquadrate (basal processes) and the presence of a median posterior parasphenoid, over the exposed ventral neurocranium.

In *Chirodipterus* there is a well-marked canal and groove system for the passage of the first efferent arterial arch, cutting through the posterior portion of the palatoquadrate. This vessel is more free in *Dipnorhynchus.* In the palate of *Chirodipterus* the entopterygoids reach backward as far as the glenoid articulation. In *Dipnorhynchus,* as previously noted, there is an area of exposed quadrate opposite a small shelf on the hind margin of the lower jaw forming the attachment for a palatomandibular ligament.

GENERAL COMPARISON. Two points of general interest with respect to the comparison of fossil dipnoan skulls may be made here. The first is that in all known forms the position of the narial apertures and the arrangement of the nasal apparatus are similar. Particularly, the nares are always on the underside of the snout and

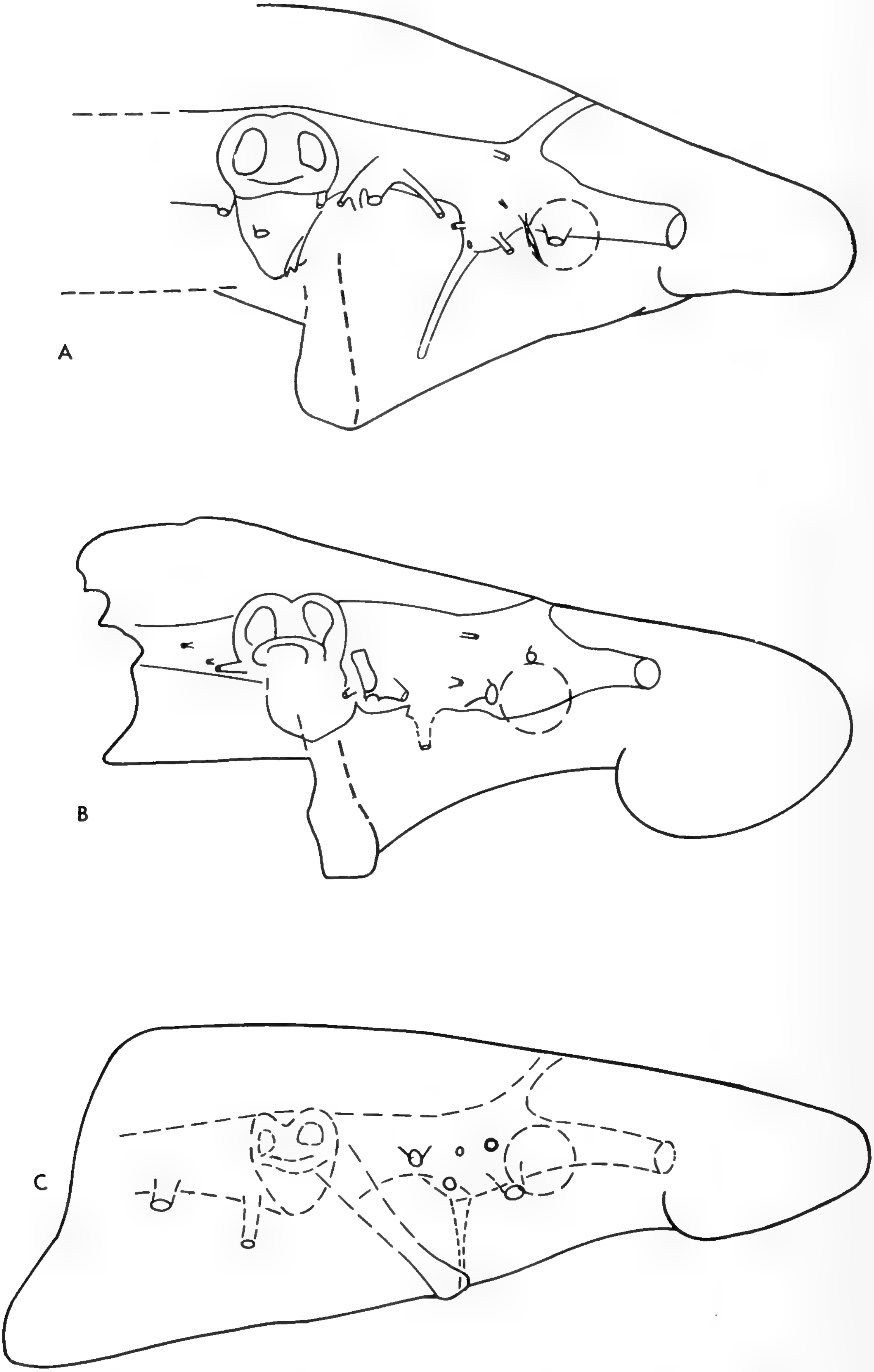


FIG. 33. Comparison of the proportions of the braincase in three Devonian Dipnoi: A) *Dipnorhynchus sussmilchi;* B) *Chirodipterus wildungensis* (after Säve-Söderbergh, 1952); C) *Dipterus valenciennesi* (reconstruction after data in White, 1965).

the snout always overhangs the oral opening. It has been suggested previously (Thomson, 1965; Panchen, 1967) that the ventral orientation of the nares in Dipnoi is a primitive feature. The present evidence offers some slight additional support for this view. There is no evidence in the newly available materials of primitive Dipnoi that the nares have migrated from a more "normal" osteichthyan position on the lateral surface of the head (cf. Jarvik, 1942; Lehmann and Westoll, 1952). Obviously this arrangement of the nasal apparatus must be connected with the lack of a marginal dentition in the Dipnoi.

The second point of general comparison involves the relative proportions of the skull in early Dipnoi. This has been a problematic subject, with several authors offering opposing views of both the evidence and its interpretation (Westoll, 1949; Denison, 1968a; Jarvik, 1968). The principal questions have concerned the relative proportions of the otic region of the skull and of the cheek. However, it is necessary here to draw attention to the relative proportions of the entire braincase in the available early Dipnoi. In Figure 33 the principal features of the braincase (nasal capsule, cranial nerve foramina, otic capsule, together with the position of the fused posterior wall of the palatoquadrate) are compared in *Dipnorhynchus, Chirodipterus,* and *Dipterus,* with details of the endocranial cavity included for the first two genera. It will be seen from Figure 33 that—despite Westoll's interpretation (1949) that the otic region becomes shorter in the early history of the Dipnoi and Jarvik's opinion (1968) that it becomes longer—the new evidence shows that the proportions of the braincase in these forms are essentially constant. There are, indeed, small differences in the position of the optic nerve foramen and the angle of the posterior wall of the palatoquadrate. The latter is obviously responsible for the changes in the proportions of the dermal cheek series. There are also differences in the relative size of the nasal capsule. However, this series of three genera, in which there is a considerable change in the pattern of the dermal skull bones, gives no evidence here of any incipient phyletic trends in braincase proportions.

Since these are the only fossil Dipnoi in which the details of the braincase and cranial nerve foramina are known, it is methodologically invalid to attempt to draw any phyletic inferences from comparison of these forms and the living genera. It may well be true (Säve-Söderbergh, 1952; cf. Jarvik, 1968) that the labyrinth cavity in *Neoceratodus* is slightly bigger than in *Chirodipterus,* but this is obviously not *by itself* evidence of a general trend toward increase in the relative size of the otic region during the period between Devonian and Holocene.

EMBRYOLOGICAL ANALYSIS OF BRAINCASE

In view of the considerable morphological significance of the structure of the skull of *Dipnorhynchus* and of primitive osteichthyans in general (see, for example, Schaeffer, 1968), it seems worthwhile to attempt to analyze the complicated holostylic skull of *Dipnorhynchus* in terms of the probable embryonic components.

In the nasal region, identification of the principal embryological components that have entered into the formation of the adult structure is relatively simple. The trabeculae of the anterior neurocranium pass forward probably fused as trabecular horns into the nasal region. The internasal trabecular extension curves forward dorsally between the nasal organs forming the dorsal portion of the internasal septum preserved as bone in the fossil. From this ethomoidal plate a cartilaginous septum possibly extended ventrally to complete the internasal septum between the anteromedial portions of the nasal organs. Anteriorly, the trabecular region curves ventrally and then the lateral horns curve laterally to form the anterolateral corner of the roof of the nasal cavity anterior to the anterior naris.

It has been noted in a previous study (Thomson, 1965) that the contribution of the trabeculae to the internasal septum differs in the living Dipnoi. In *Protopterus* and *Lepidosiren* the anterior portions of the trabeculae fuse to form a median structure which curves dorsally over the internasal region. A secondary septum then reaches down ventrally between the nasal sacs to form the internasal septum. Anteriorly the trabecular portion curves ventrally again and gives off the trabecular horns. In *Neoceratodus* the trabeculae reach directly forward in the floor of the nasal region and the internasal septum is developed as a dorsal extension from them. The preserved portion of the incomplete internasal septum of all known fossil Dipnoi *(Dipnorhynchus, Uranolophus, Ganorhynchus,* and *Chirodipterus)* is arranged in the same way as in Lepidosirenidae, with a dorsal band of tissue curving over the nasal region. It seems a reasonable conclusion that the preserved portion of the internasal septum in these fossil forms actually represents material of trabecular origin. In this case, the arrangement of the trabeculae in the internasal region of *Neoceratodus* must be considered as secondary.

The prominent ventral bar of the postnasal wall is formed by the processus antorbitalis from which a dorsal lamina extends to form the postnasal wall around the profundus canal. The lateral wall of the capsule is formed by the fusion of the processus antorbitalis with the recurved trabecular horn. They fuse dorsal to the narial apertures and there is accordingly no continuation of this lateral wall ventral to this level. The processus antorbitalis also has a posterior distal fork that forms the buttresses against the undersurface of the skull roof. It would perhaps be an optimistic anatomist who would find homology between the forked end of the processus antorbitalis in *Dipnorhynchus* and that in *Lepidosiren* (as described by Agar, 1906a).

The strong direct connection between the undersurface of the postnasal wall (lamina orbitonasalis) and the visceral palate might perhaps be construed as evidence for the suggestion by Jarvik (1954; cf. Bertmar, 1963) that the lamina orbitonasalis in fishes is of visceral origin.

In the orbital region the separation between palatoquadrate and neurocranial components probably ran on a horizontal level ventral to the optic foramen. In the temporal and otic regions the separation is more difficult to determine. The jugular canal seems to be formed by the apposition of a processus ascendens palatoquadrati laterally with the neuroranial wall medially. The maxillary-mandibular fifth nerve foramen marks the separation between the processus ascendens and processus oticus palatoquadrati. The latter is fused to the anterolateral wall of the otic capsule and forms the lateral wall of the posterior section of the jugular canal. The dorsal extent of the processus oticus cannot be determined, but presumably the dorsolateral crista of the endocranium is a neurocranial structure. As we have seen, the trigeminofacialis ganglion complex lies dorsal to the jugular canal, but it must be considered to be enclosed laterally by both the processus ascendens and processus of the palatoquadrate, with the maxillary-mandibular foramen between them. The question of whether there is a lateral commissure or a cavum epiptericum is formed between the palatoquadrate and neurocranium is one that cannot be answered until the homology of the "otoquadrate bar" has been decided.

Ventrally, the palatoquadrates are extremely thick underneath the otic region and are greatly expanded both toward the midline where they fuse beneath the neurocranium (enclosing the internal carotid arteries) and posteriorly where they are seen to spread backward underneath the otic region. The expanded medial parts of the palatoquadrates correspond to the basal palatal processes and their extreme enlargement essentially obliterates the basal plate of the trabecular neurocranium. It will be noted, from the posterior position of the hypophyseal recess and canal and the position of the tip of the notochord, that the trabecular portion of the neurocranium extends far posteriorly, to approximately the level of the center of the inner ear cavity. Underneath the occipital region the paired ventral structures presumably represent the main parts of the parachordals on either side of the notochord.

The trigeminal and facialis nerve ganglia are enclosed in a portion of the braincase wall, the outer part of which is probably palatal in origin. The jugular canal also is enclosed laterally by the palate. However, a point of difference from other fishes is that none of the fifth nerve rami pass directly into the jugular canal, the course of which lies morphologically ventral to the level of the ganglion complex. The profundus nerve only enters the jugular canal at the anterior jugular foramen. The ramus hyomandibularis VII passes posteriorly into the jugular canal. Both nerves seem to pass for a distance within the substance of the braincase wall dorsally and slightly medially of the jugular canal. The possibility exists that this portion of the braincase wall, immediately ventral to the trigeminofacialis ganglion pocket, is formed embryonically of two parts, medial neurocranial and lateral palatal structures—between which the previously mentioned nerves pass.

BRANCHIAL SKELETON OF *DIPNORHYNCHUS SUSSMILCHI*

In the material that we have prepared there is a single element that we have tentatively identified as a portion of the hypobranchial skeleton. This small element is illustrated in Figure 34 (reconstruction) and in Figure 90a, b, c. Although incomplete, the specimen represents a portion of a bilaterally symmetrical element that we assume to have been a basibranchial located in the ventral midline. It consists of a central disc, dorsally concave, to which a series of rod-shaped elements (the tips of the hypobranchial elements) were attached. One such element is preserved in natural association on the right-hand side. A facet showing the position of attachment of a symmetrical left element is clearly shown. In addition, on the ventral face of the disc there is a median facet that formed the site of attachment of a more ventral element (presumably a urohyal) pointing directly backward in the midline. The base of the preserved portion of the right hypobranchial shows a further site of attachment, presumably for the next most anterior arch. Anteriorly, the disc-shaped base is incomplete; we imagine that it was attached to a more anterior basibranchial. In our interpretation, the preserved element supported the urohyal and branchial arches IV and V. The anterior basibranchial supported the remaining elements.

The branchial skeleton of other Palaeozoic dipnoans is, unfortunately, unknown.

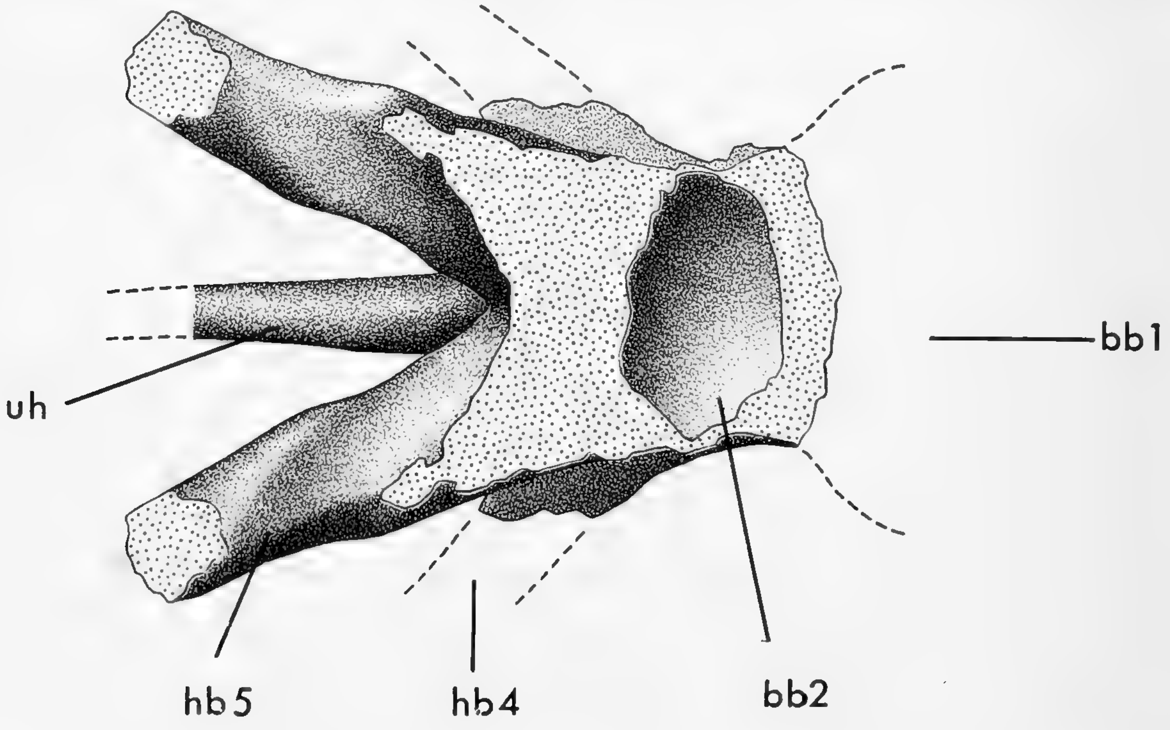


FIG. 34. *Dipnorhynchus sussmilchi*. Reconstruction of portion of the hypobranchial apparatus, based on specimen P 13837, National Museum, Melbourne.

SQUAMATION OF *DIPNORHYNCHUS SUSSMILCHI*

Two different types of scales of *Dipnorhynchus sussmilchi* are available for study. Several rhombic flank scales were discovered in association with the lower jaw from Buchan (P 13837), a single incomplete flank scale was embedded in the matrix on specimen F 10813 [this was interpreted by Hills (1933) as forming part of the denticulation of the palate], and an isolated median dorsal ridge scale was collected as Taemas (1970D) by Dr. J. A. Warren. The scale structure is illustrated in Figures 86 to 89.

The flank scales show a remarkable structure, for dipnoans, in that they articulate one with another by means of the "peg-and-socket" arrangement that was long ago considered diagnostic of the "ganoid" fishes (see "Discussion"). The dorsal margin of each scale is produced into a short roughly triangular "peg" which fitted into a simliarly shaped depression in the ventral part of the undersurface of the scale in the next row. The depression or "socket" is actually formed on a broad dorsoventrally directed thickened band on the internal face of the scale. The "peg" is the dorsal projection of the thickened band beyond the margin of the scale surface. The surface of this median thickened band of tissue is marked by a series of parallel ridges (Fig. 86b).

The external face of the scale is formed in two discrete areas. The anterior portion of the scale—the narrow area that was overlapped by the scale in front—is covered with closely spaced, flattened dentine tubercles. This tuberculated area extends dorsally in a narrow band just at the base of the "peg" process. The exposed portion of the external face of the scale is cosmine covered, and "Westoll-lines" may be observed. In certain cases, abrasion of the surface of the scale has removed part of the cosmine surface, and the denticulated dentine layer beneath is revealed (Fig. 89a). The histological nature of these features is described below.

The rhomboid shape of the scale and the "peg-and-socket" type of articulation has been described in the Middle Devonian osteolepid rhipidistians *Gyroptychius* and *Osteolepis (*Jarvik, 1948). It has also very recently been described in the primitive lungfish *Uranolophus* (Denison, 1968a, b). Like *Uranolophus, Dipnorhynchus* lacks the groove separating the cosmine-covered and denticulated areas on the outer face of the scale which is seen in the above-named rhipidistians. But whereas the ridge on the inner surface of the scale is "weak or absent in *Uranolophus*" (Denison, 1968a), it is as well developed in *Dipnorhynchus* as in Rhipidistia. The overall similarity in general structure of the scales of these forms is most striking as is the difference between this type of scale and that seen in the later Dipnoi.

NOTES ON BONE HISTOLOGY OF *DIPNORHYNCHUS SUSSMILCHI*

We have already noted that cross sections through the massive palate of *Dipnorhynchus sussmilchi* show that it is composed primarily of a thick layer of spongy endochondral bone on the ventral surface of which is a layer of dentine. There was possibly an external enameloid or durodentine layer, but the preservation makes the identification uncertain. The dorsal surface of the palate was formed by a thin perichondral bone layer.

We have made thin sections of a portion of the surangular bone of specimen P 13837 from Buchan. The basal layer of the dermal bone is made up of lamellar bone showing cross striations; next there is a fairly thick layer of spongy bone; and on top of this lay dentine and cosmine layers. On the dentary, the tip of the snout, and most of the surface of the prearticular there was an enamel surface.

The composition of the scales is generally similar to that of the dermal bones. There is a very thick lamellated, cross-striated basal layer separated by a thin spongy bone layer from the more external dentine. The dentine seems to be orthodentine. The surface of the shiny exposed portion of the scales is formed of cosmine. The tubercles on the overlapped portion of the external surface are formed of dentine only. Under the smooth cosmine layer, several generations of overgrown denticles may be seen. The "Westoll-lines" may also be detected in thin sections.

These notes are unfortunately brief owing to the less than perfect state of preservation of microscopic detail in the material. In every feature that has been examined, however, the histology shows a remarkable resemblance to that seen in *Uranolophus* and described by Denison (1968a). As far as we can tell, Denison's observations on structure and growth in *Uranolophus* must apply equally to *Dipnorhynchus*. The occurrence of an enamel layer on the snout, dentary, palate, and prearticulars seems to be a common phenomenon in Devonian Dipnoi.

NOTES ON SOFT ANATOMY OF *DIPNORHYNCHUS SUSSMILCHI*

Reconstructions of the soft anatomy of a fossil organism are, of course, highly tenuous and usually suffer from the fact that they are based on extensive extrapolations from conditions in living forms. However, it is important that attempts at reconstruction be made and accordingly we present the following notes on selected aspects of the soft anatomy of *Dipnorhynchus.*

NASAL ORGAN. As already described, the nasal organ lies in a nasal chamber that is partially subdivided into three main portions—a principal posterior chamber and smaller anteromedial and anterolateral chambers. These chambers must reflect a similar subdivision of the nasal organ itself. The anterolateral chamber is directed anteriorly towards the notch in the margin of the snout that must have (partially) enclosed the anterior naris. The position of the posterior naris is not indicated by such a notch, and we may be certain that the posterior naris must have been situated in the ventral part of the principal posterior portion of the nasal organ. An important feature to notice is that both the narial openings are completely ventrally directed and the position of the nares is identical with that in other Dipnoi. It is difficult to assign a particular functional significance to each of the three subdivisions of the nasal organ. The anterior recess seems to be principally the anterior portion of the original "nasal groove." The position of the posterior naris given in the restorations (Fig. 27) places the posterior end of the nasal groove at the junction between the end of the anterolateral portion of the nasal organ and the posterior portion. The latter is clearly the main sensory region of the nasal organ and possibly contained a rosette of olfactory surfaces. The olfactory tract enters the principal posterior section directly; the fact that the canal for the tract is subdivided by a thin vertical septum probably indicates that the dendritic branching of the olfactory tract over the whole of this sensory region occurs in the rearmost part of the nasal cavity. Although it would be tempting to try to identify a structure corresponding to Jacobson's organ in *Dipnorhynchus,* there is no justification for this. In fact, the existence of such an organ in living Dipnoi, or indeed any fish, is to be doubted (see Rudebeck, 1944; Thomson, 1965).

ACOUSTICOLATERALIS SYSTEM. The general structure of the inner ear and the cranial lateral line system of *Dipnorhynchus* have already been described previously. However, two aspects of the acousticolateralis system require further treatment.

SPIRACULAR SENSE ORGAN. In the preceding description of the otic region of the skull, we have identified a spiracular recess that we believe contained a spiracular sense organ leading from the spiracular cleft, the cavity of which was continuous with that of the pharynx. This identification is based upon the following pieces of evidence.

1) Its overall position is between the hyoid arch (behind) and the palatoquadrate (in front).

2) The hyomandibular ramus of the seventh nerve passes into the cleft.

3) Apart from the connection via the seventh nerve canal, there is no connection between the blind cleft and the neurocranial cavity, nor does it connect with the orbitotemporal cavity. Thus it cannot be the passage for any blood vessel.

4) A small ramus oticus VII passes into the posterior part of the spiracular cleft.

5) The internal faces of the cleft are extremely smooth, as if some soft structure were contained therein.

6) A spiracular sense organ has been identified in *Protopterus* and *Lepidosiren* (Agar, 1906b). A blind spiracular cleft has been described in embryos of *Neoceratodus* (see Fox, 1965). Although such an organ is not found in any other fossil dipnoan it is not an uncommon feature in other primitive fishes (Crossopterygii, *Amia, Lepisosteus,* etc.).

ROSTRAL TUBULI. As previously mentioned, at the tip of the snout and of the mandibular symphysis there are large external pores opening into a series of ramifying tubules which do not form part of the lateral-line system. These tubuli are formed of a perichondral bone sheath; they extend internally to open into the nasal cavity and Meckelian vacuity respectively, where they appear to receive a vascular supply and innervation from the fifth and or seventh nerves or both. The tubules are arranged very differently from the canals and pits that held neuromasts of the lateral seismosensory system. The rostral tubuli clearly housed a sensory system, but one may only guess at its specific function. Possibly it was in some way similar to that of the organs of Lorenzini.

DISCUSSION—EVOLUTION OF THE DIPNOI

Dipnorhynchus AND THE PHYLETIC POSITION OF THE DIPNOI. The question of the phylogenetic position of the Dipnoi has long been debated both with respect to their relationship to fishes in general and to the Amphibia in particular. It is now generally agreed that there was no direct relationship between Dipnoi and Amphibia (however, see Fox, 1965, for recent arguments in favor of such a link). But even after it had been found that the rhipidistian crossopterygian fishes provided a closer link to the earliest tetrapods than the Dipnoi, the problem of evaluating evidence for a possible dipnoan-crossopterygian relationship remained. Some workers, for example Goodrich (1909) and Woodward (1891), have classified the Dipnoi near the Arthrodira. Others, (particularly Westoll, 1949) have defended the concept of a natural assemblage containing the Dipnoi and Crossopterygii, and Romer (1955) coined the term "Sarcopterygii" for this group. Romer's view has prevailed with the majority of workers, but more recently Jarvik (e.g., 1964) has revived the possibility of a closer link of the Dipnoi to "elasmobranchiomorphs." White (1965, 1966) concurred with Jarvik, stressing particularly the distinctness of the dermal skull roof pattern and dentition. Bertmar (1968) argued that the closest relationship was between Dipnoi and Actinopterygii. Even more recently, Denison (1968a, b) and Schultze (1970) have brought forth new evidence that supports the sarcopterygian concept. The structure of *Dipnorhynchus sussmilchi* also provides strong evidence for a direct dipnoan-crossopterygian relationship (see also Thomson, 1969).

In comparison with other fishes, one fact is clear from the outset—that *Dipnorhynchus* is typically dipnoan. It has a primitive but nonetheless characteristically dipnoan skull roof and an apparently very primitive dipnoan dentition. However, it must be noted at the same time that in certain features *Dipnorhynchus* shows a structure that is not found in other dipnoans, but that is more typically found in the Crossopterygii. From these features we conclude that *Dipnorhynchus* is extremely primitive and shows evidence of a close phylogenetic relationship to the Crossopterygii or, more realistically, to the immediate ancestors of that group. We may now consider these in detail and try to assess their significance.

SCALES. The new descriptions of *Dipnorhynchus* and also *Uranolophus* (Denison, 1968a, b) have provided further new evidence of dipnoan-crossopterygian similarity. The microscopic structure of the scales, revealing traces of several generations of overgrown dentine tubercles, is remarkably similar to that described for the early rhipidistian *Porolepis* (Gross, 1956). The major structural features, particularly the "Westoll-lines" that show the manner of growth of the cosmine layer, and the peg-and-socket articulations between scales is the same as those seen in such Middle Devonian osteolepid rhipidistians as *Gyroptychius* [see also discussion by Denison (1968a, b)].

CHEEK. Whereas the cheek in all previously known Dipnoi is relatively short, *Dipnorhynchus* has a longer cheek, more readily comparable with that of other fishes such as the Crossopterygii. An important feature of the cheek is the presence of a short "preopercular" lateral-line canal in addition to the infraorbital canal.

LOWER JAW. The structure of the lower jaw in most dipnoans shows almost no resemblance to the lower jaw of other osteichthyan fishes, both with respect to the general arrangement of the dermal bones and the unique dental plates. The arrangement of the dermal bones of the jaw in *Dipnorhynchus* (and possibly *Uranolophus*), as we have seen, is more primitive than that of other dipnoans, but a scheme of evolution may be drawn up linking the structure of *Dipnorhynchus* and later forms in a common pattern (Fig. 24). Most importantly, it is also possible to see in the structure of *Dipnorhynchus* clear links with the arrangement in Crossopterygii. In Fig. 24 we compare the external dermal bones of the lower jaws of *Dipnorhynchus* and the rhipidistian crossopterygian *Holoptychius*. It is most remarkable how similar the two forms are, the only major divergence being in the relative development of the dentary, which in *Holoptychius* extends along almost the entire dorsal margin of the jaw and is readily correlated with the presence of a marginal dentition in Crossopterygii. A most striking point of similarity is the fact that the surangular in *Holoptychius* (though by no means in all crossopterygians) bears a short anterodorsal branch of the lateral line that is possibly homologous with the oral lateral line that in *Dipnorhynchus* is carried on the large surangular all the way to the anterior union with the mandibular lateral line. Although they had probably evolved separately from a common ancestor, one might easily suppose that the elongate *Holoptychius*-type of jaw evolved from the *Dipnorhynchus*-type by reduction of the surangular, enlargement of the dentary, and reduction of the symphysis. Although it is rather too early to decide which pattern is the more primitive, the presence of a full oral and a mandibular lateral line in the dipnoans raises the interesting possibility that this is the more primitive condition. Further it is possible that the dentary was originally a small anterior element, which only assumed its modern aspect as the principal tooth-bearing element of the lower jaw in the Osteichthyes as a specialization. A further point of resemblance between *Dipnorhynchus* and other Osteichthyes with respect to the lower jaw is the presence of a full Meckelian fossa (reduced in later Dipnoi).

In summary, despite the obvious differences in the dentition itself, the overall structure of the lower jaw of *Dipnorhynchus* is such as to form a common pattern with the Crossopterygii, while at the same time there are extremely clear relationships to the other Dipnoi.

These are all new evidences of similarity pointing to a direct and close relationship between Dipnoi and Crossopterygii. To these must be added Denison's (1968a, b) evidence from the structure of the postcranial skeleton of *Uranolophus* and Schultze's arguments (1970) concerning vertebral structure. When all this is added to the familiar lines of argument involving the presence of lungs, the development of the heart and brain, etc. cited by earlier authors, there is formed a substantial body of evidence suggesting (but, of course, still by no means proving) that the Sarcopterygii is a natural assemblage of closely related fishes, distinctly separated from other groups.

In order for this assessment of dipnoan-crossopterygian relationships to have authority it is necessary to provide, in addition, a satisfactory explanation of the major differences between the two groups—the differences that have led previous workers to separate them. The principal differences between the Dipnoi and Crossopterygii concern the skull (particularly the skull roof) and the dentition (see White, 1966). The characteristic nature of the skull of Dipnoi is obviously related to the phenomenon of holostyly. To understand the phylogenetic significance of these characteristics we must make some observations of the probable history of the skull in the ancestral predipnoan lineage.

Regardless of the interpretation of the "hyomandibula" in *Dipnorhynchus,* in our opinion, it seems most likely that in the immediate ancestors of this genus some mobility of the cheek upon the skull was possible (see Thomson, 1969), requiring the arrangement of an hyomandibula in a normal hyostylic or amphistylic suspension. The possible retention of a large distinct hyomandibular in the nonkinetic skull of *Dipnorhynchus* might be explained by its position, which indicates that it has taken on the function of bracing the posterior surface of the massive lateral wing of the braincase. If this is true, then it must follow that originally the palates were not completely fused. In any case, the separate parasphenoid, as developed in *Uranolophus* and possibly in *Dipnorhynchus lehmanni,* must be a primitive character that has become lost in *Dipnorhynchus sussmilchi.* However, there is no evidence to suggest that a posterior stem of the parasphenoid was present in a common ancestor. Had it been present, it surely would have been retained even in *Dipnorhynchus,* and certainly in *Uranolophus.* We may be reasonably certain that there was no posterior dermal covering in the roof of the gullet except for a pair of loose plates and the dermal elements (if any) directly associated with the branchial arches. Thus, the posterior process of the parasphenoid seen in Middle Devonian and younger dipnoans is a secondary feature. In this respect, the evolution of the dipnoan parasphenoid accords very well with Jarvik's scheme of the evolution of the parasphenoid in the Osteichthyes (1954).

The question of whether the skull in the earliest Dipnoi included an intracranial joint [such as was hinted at for *Dipnorhynchus lehmanni* by Westoll (in Lehmann and Westoll, 1952)] is impossible to decide. On the whole it seems likely that the jointed condition is a specialization of the Crossopterygii, as the holostylic condition is a specialization of the Dipnoi. However, even if an earlier dipnoan than *Dipnorhynchus* or *Uranolophus* had possessed an intracranial joint, no indication of it would be expected to be retained in these heavily holostylic forms. In the absence of more primitive dipnoans, this question must be left unresolved.

Apart from the "normal" movements between cheek, palate, and braincase that are seen in many fishes, the possibility also exists that in an early form the otic-occipital connection (represented by a sulcus in *D. sussmilchi*) also allowed some degree of intracranial flexure. In this case, the absence of a posterior parasphenoid stalk, which braces the ventral surface of this region in later Dipnoi, would further be explained. The fact that a somewhat similar otic-occipital sulcus is found in paleoniscid actinopterygians may suggest that such structures were a primitive feature of all Osteichthyes. If this were the case, then probably the crossopterygian kinesis at the trabecular-parachordal separation represents a lateral innovation.

If there were some kind of intracranial movement in ancestral dipnoans, then the very rapid evolution of the characteristic holostylic dental battery, which is evident from the stages reached by *Uranolophus* and *Dipnorhynchus,* must have taken place *after* the Dipnoi differentiated from the ancestral stock. Probably any marginal dentition was lost at a stage when it was only feebly developed—as indicated by the short dentary in *Dipnorhynchus* and the primitive ventral position of the nares in Dipnoi (see also Thomson, 1965).

If the preceding assessments are correct, then we may make two observations concerning the phylogenetic significance of the specialized dental apparatus of Dipnoi. 1) Since the dipnoan dental pattern is a specialization that probably developed *within* the Dipnoi, rather than was present in an antecedent stock, it would be wrong to argue that this characteristic provides evidence that the Dipnoi and Crossopterygii (a group within which this particular specialization has not developed) are unrelated. 2) It also follows that any apparent similarity between the dental batteries of Dipnoi and other fishes is due to convergence rather than direct relationship.

The second major point of difference between the Dipnoi and the Crossopterygii is, of course, the nature of the skull roof. The problem resolves into two alternatives: either the dipnoan skull roof reflects an ancestral situation from which the crossopterygian condition could not have evolved, or the dipnoan condition is a specialization of the dipnoan lineage alone—in which case a dipnoan-crossopterygian relationship is not precluded. Some authors (for example, White, 1966) have considered the dipnoan skull roof pattern to be so different from that of crossopterygians as to indicate a long separation in ancestral history. Others (for example Westoll, 1949) have sought to develop schemes in which hypothetical predipnoan and precrossopterygian patterns might indicate a common ancestry of the two groups, or even the development of one pattern from another. Such schemes have been criticized recently by Jarvik (1968). It seems to us that the phylogenetic significance of a given pattern of dermal skull bones can only be understood in terms of the functional history of the whole skull. The pattern of the skull roofing bones is obviously subject to adaptive modification, like any other biological system.

All currently accepted theories concerning the development of the dermal skull pattern in vertebrates postulate the development of individual bones from a series of initial primordia around which bone is deposited. The question of "fusion" and "elimination" need not concern us here. However, it will be agreed, we believe, that regardless of the *manner* of formation of the bones, the development of any *pattern* must be controlled by, and adapted for, specific mechanical conditions. It must then follow that the dermal bone pattern in Dipnoi—essentially a mosaic with progressively larger bones toward the rear of the skull—also reflects a particular mechanical condition. Further, it seems most productive to interpret the dermal skull pattern with reference to the single most obvious feature of the cranial anatomy of Dipnoi—holostyly.

We may follow a single hypothesis with respect to the formation of dermal skull patterns: that the development of a particular pattern of dermal elements is a function of particular highly directional stresses acting in the skull as a whole. In any skull roof, where strictly oriented stresses and strains are developed due to muscular action and the relative movement of palate, braincase, and branchial arches, there seems to be a tendency for larger, specially shaped elements to occur. In the opposite case, where there are no strictly oriented forces, a mosaic of elements tends to appear. The latter is seen quite clearly in the solid snout region of many primitive vertebrates. The situation may also be modified by a separate evolutionary tendency for the number of elements in the skull roof to be diminished and for the relative size of individual elements remaining to increase, as indeed occurs in Dipnoi. The early dipnoan pattern, with a mosaic in the anterior region of the skull and in the cheek simply reflects the immobility of these regions and the underlying tissues. Probably the larger size of bones B and C in the dipnoan skull reflects the forces developed by the adductor muscles in the chamber immediately beneath these bones which are partly inserted on them. Similarly, the shape of C, B and I may be interpreted as a direct consequence of the fact that they overlay the mechanically important dorsomedian and dorsolateral cristae of the braincase. These principal characters of the dipnoan skull may be traced with small modifications (owing in part to a general decrease in ossification) throughout all lineages (see discussion of skull roof, p. 19 *ff.*, and below). The importance of their relationship to functional characteristics of the skull as a whole can scarcely be overemphasized. This type of simple mechanical analysis can be continued further and is an important tool in the interpretation of dermal bone patterns of vertebrates (Thomson, in preparation).

If the preceding is correct, then it also follows that dermal bone patterns must change as systems of cranial mechanics change. While, clearly, any given pattern must develop from a pre-existing pattern, the fact that each pattern develops ontogenetically from a mosaic condition allows modification of a pattern to proceed readily. This is particularly the case when a newly developed system of mechanics requires reversion to a mosaic rather than evolution of a new highly directional pattern of skull elements. In our estimation, therefore, all that may be inferred from the condition of the skull roof in primitive Dipnoi is that the dermal bone pattern is functionally integrated with the holostylic condition of the braincase and palate. In view of the strong likelihood that the anscestors of the Dipnoi had a hyostylic or amphistylic skull, we must conclude that, like the palate, the highly specialized condition of the skull roof in Dipnoi (as we presently know them) should not be expected to offer evidence concerning the ancestral relationships of the group. It is a product of dipnoan evolution alone.

All this is simply an affirmation of the simple and fundamental principle that continuity of structure is only possible where there is also continuity of function. In phylogenetic considerations, a discontinuity in structure is therefore not necessarily an indicator of broad phyletic separation; it may reflect a change in function within a single group. In case of the Dipnoi, a major change in cranial function has involved a complete remodeling of the skull and the "derived" dipnoan group is rather different in certain features from its sarcopterygian relatives. With respect to the lower jaw there is less difference in function and the dermal bone pattern shows closer similarities between the two groups. Once we have seen the functional basis of the unique cranial characteristics of known Dipnoi, we are able to assess their phylogenetic significance in comparison with other more conservative characteristics. Thus, we believe that the evidence of morphological similarity, for example, in the scales, cheek, lower jaw, and postcranial skeleton between early dipnoans and the Crossopterygii, is of greater significance than the more obvious differences between the two groups.

EVOLUTION OF PALAEOZOIC DIPNOI. At present, discussion of evolutionary relationships within the Dipnoi themselves must depend mainly on details of the skull roof and the dentition, though some information on the mandibles can now be added. Certain assumptions will be made in the discussion that follows, and they are now explicitly stated. Some of them follow naturally from what has been said on bone homology earlier; others depend on evidence that is not conclusive, but which seems to be reasonably safe.

1) In determining relationships between genera, the roofing bones associated with the braincase and palatoquadrate are likely to be more important than the other roofing bones.

2) Bones lost from the roof are unlikely to be regained.

3) From Early to Late Devonian, there was a common pattern of reduction of the lateral-line bones lateral to B and the posterior part of C. At first this occurred through reduction in the size of the Y, X, K, and J elements, and subsequently by loss of K and of one of the Y bones. This pattern implies a common ancestry for these forms with slight diversification of the basic holostylic cranial mechanism.

4) The shape and number of the fins are unlikely to be of greater significance for understanding evolutionary relationships than the structure of the roofing bones of the skull. There is too great a possibility for convergent or parallel evolution in fin structure in accordance with particular modes of swimming (see Thomson, 1969).

5) The character of the teeth is clearly related to mode of feeding. There seems to be no inherent reason why animals of a single stock should not diversify their feeding habits and therefore their dentition. This could involve either the gain or loss of denticles or of a tooth pattern. Given our present knowledge of the Dipnoi, the nature of the dentition alone is not necessarily a reliable guide to phylogenetic relationship (cf. Denison, 1968a, p. 386). This point can also be demonstrated empirically by appeal to *Uranolophus* and *Dipnorhynchus*. These are the earliest known dipnoan genera, and have skull shapes, dermal roofing bone and mandibular dermal bone patterns, palatal structures, anterior mandibular furrows, and Meckelian vacuities so similar that it would be difficult to deny that they are closely related. Yet they have very different dentitions.

6) The size and shape of the mandible and its muscle insertion areas will also be related to method of feeding and should not be used in preference to dermal bone patterns to indicate relationships.

7) The form of the parasphenoid, being the base of the braincase, is likely to be important.

In the following discussion of the general course of dipnoan evolution, we are obviously unable to document precisely the origin and relationships of particular known fossil genera. However, the citing of these genera offers the only convenient means of indicating the relationships of the lineages of which we believe they formed a part.

The Early Devonian genera *Uranolophus* and *Dipnorhynchus* are at a similar level of development in numerous characters—the multiplicity of roofing bones anterior to D; the large size of X and K; the small size of L; the junction of the I bones behind B; the extension of the supra-orbital canal from K into J; the presence of at least two O bones; the lack of a junction between the canals in X and K; the long cheek; the lack of a parasphenoidal stalk; large lower jaw; well-ossified Meckelian cartilage; similarly arranged dermal bones and lateral-line canals in the lower jaw. All these characters may fairly be regarded as primitive. However, *Uranolophus* is distinct in having large E bones that are in contact with C; a fairly large D; no pineal foramen; a marginal tooth row and denticulate palate and prearticular. The evidence is not strong one way or the other, but the character of the D and E bones suggest that *Dipterus* was derived from a *Uranolophus*-like rather than a *Dipnorhynchus*-like form despite the fact that the former is older. This is interesting in view of the freshwater habitat of *Dipterus* and *Uranolophus.*

The transition from *Uranolophus* to *Dipterus* involves the reduction in size of K and X as the eye moves back and the cheek shortens; the parting of the I bones behind B; the reduction of the number of bones in the snout; the reduction of the number of O bones to one; the increase in size of the L and M elements; the junction of the infra- and supra-orbital canals between K and X; the capture of the occipital commissure by I and the loss of H; the development of ceratodont dentition and a parasphenoidal stalk; the close approach of the oral and mandibular canals with a modification of the angular-surangular relationships; and the reduction of the Meckelian vacuity.

From *"Dipterus,"* three stocks radiate into the Upper Devonian—one to *Scaumenacia* and *Phaneropleuron;* a second to *Fleurantia, Soederberghia, Oervigia* and *Jarvikia;* and a third to *Rhinodipterus secans.* In view of the fact that certain of the genera grouped together here have previously been considered to be in different groups (e.g., *Phaneropleuron* and *Scaumenacia* are placed in different Orders by Lehman, 1959, by virtue of their different fin arrangement) some justification of this phylogeny is necessary. The similarity of the skull roof in *Scaumenacia* and *Phaneropleuron* has been noted by several authors (Westoll, 1949). In both, the bones B, C, and E are greatly enlarged, but D is lost; K has disappeared from most specimens of *Scaumenacia* and many specimens of *Phaneropleuron;* and both have ceratodont dentition. The main differences are in the relatively larger size of L and the development of a single dorsocaudal fin in *Phaneropleuron.* Both these differences can be easily accounted for by evolution along established dipnoan trends, *Phaneropleuron* being the younger form. The presence of K in a higher proportion of specimens of *Phaneropleuron* than *Scaumenacia* suggests that they are not on the same line of descent. Little is known of the late Givetian genus *Pentlandia,* but there is no reason at present to doubt the view of Watson and Day (1916) that it is closely related to *Scaumenacia.*

The *Fleurantia* stock is characterized by an elongate head, the loss of K and D, the occasional complication of C, the enormously long L and E and the very long parasphenoid with a bifid termination of its posterior stalk. *Soederberghia* is probably the end product of an early offshoot from this stock. It retains the lateral-line canal (rather than a pit line) from X to J and it has a pair of bones on the infra-orbital lateral line below X occupying the position of 4, but neither of them is in contact with the orbit. These features are not known in any other dipnoan. All its other characteristics, except its almost smooth palate, ally it with the *Fleurantia* stock. It is possible that the main part of the stock developed through *Rhinodipterus ulrichi.* (For a discussion of *R. ulrichi* and *R. secans,* see p. 37).

The third main stock is represented by *Rhinodipterus secans.* This has retained many of the characters of *Dipterus* that are lost, or partly lost, in the other two, e.g., bones D, O, and K and the continuation of the lateral-line canal from K to J. On the other hand it has a posteriorly projecting I and a long posterior parasphenoidal stalk, differentiating it from *Dipterus.* The only known material occurs in the lower Famennian and is thus coeval with *Fleurantia* and *Scaumenacia.* The importance of this stock is that it provides the only possible origin for the Early Carboniferous and later genera (all of which retain D) unless one is prepared to admit the possibility of the redevelopment of a bone in the D position in the *Scaumenacia* stock. This we do not accept.

Two stocks are present in the Lower Carboniferous—the *Ctenodus* stock and the *Sagenodus* stock. The former is characterized by relatively large paired C and E with a smaller D at the angle of junction of these four bones. In the latter stock C has atrophied and the vacated space is occupied by a forward extension of B and an enlargement of D. Both exhibit a number of features absent from all Devonian forms: with the doubtful exception of *Conchopoma* all genera show the capture of the occipital cross commissure by B and the incorporation of Z in the skull table. The parasphenoid, in all genera in which it has been observed, namely *Sagenodus, Conchopoma, Uronemus,* and *Ctenodus,* has a flatter rather massive anterior rhombic portion that lacks a continuation of the groove present on the

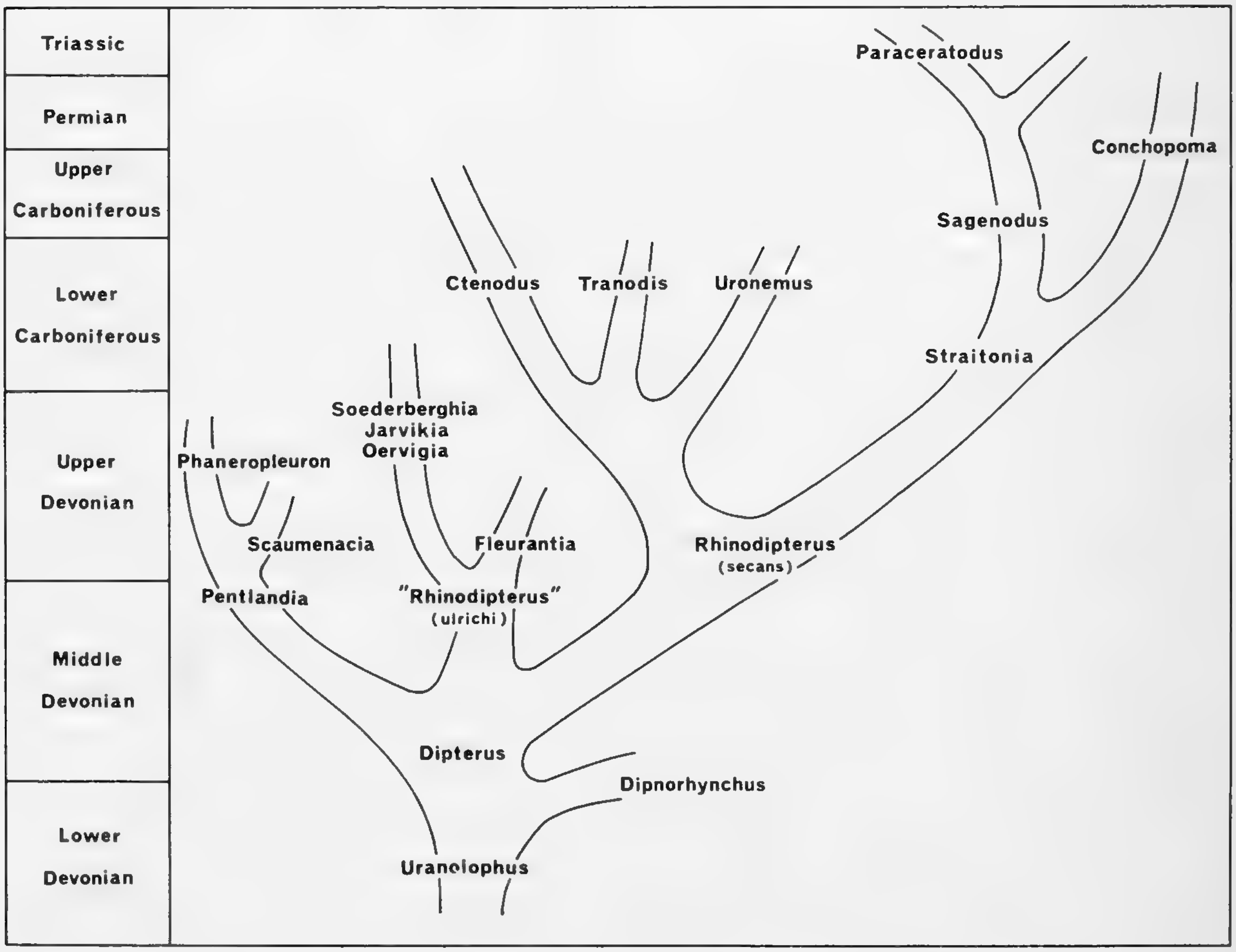


FIG. 35. Phyletic relations of known Paleozoic Dipnoi in the light of the present discussions.

ventral surface of the posterior stalk. In addition, the termination of the parasphenoidal stalk, at least in *Sagenodus* and *Ctenodus,* is rounded rather than bifid. These features suggest that the two stocks had a common origin during the Late Devonian or perhaps the Early Carboniferous, and that they have adopted basically different means of reducing the number of roofing bones. Within each stock the dentition shows a wide range of variation. *Sagenodus, Ctenodus* and *Tranodis* are ceratodont; but *Uronemus* and *Conchopoma* have a large number of small teeth covering the palate, and in addition *Uronemus* has a row of compressed marginal teeth. Some workers have thought that *Uronemus* and *Conchopoma* are probably related because of their similar dentition. However, in *Uronemus* the biting surfaces are apparently restricted to the pterygoids while in *Conchopoma* the pterygoids are very narrow and the enlarged parasphenoid carries most of the denticles, suggesting that the two genera represent entirely separate adaptations to the same mode of feeding.

The main line of development to the Mesozoic *Ceratodus* was through the *Sagenodus* stock. Carlson (1968) has already argued cogently in favor of this view using roofing-bone data similar to ours.

This evolutionary scheme (Fig. 35) is different in many respects from those recently proposed by various authors, and it has certain important taxonomic implications. Bertmar (1969) has attempted to construct a phylogeny of the Dipnoi. His discussion lacks detail and depends in part on questionable evidence such as the presence of maxillaries and premaxillaries in certain Devonian genera; the use of a longer snout to indicate relationships in the absence of data on the skull structure in others; and the use of the structure of the endocranium to trace the lineages of the Ceratodontidae and Lepidosirenidae back to *Chirodipterus,* when in fact the roof of *Chirodipterus* is unknown and hitherto its endocranium has been the only Paleozoic one that has been reasonably well known. As might be expected from what has already been indicated, there is little agreement with the classification of Lehman (1966) which, at the ordinal level, is based entirely on fin arrangement. There is a measure of agreement with the scheme proposed by Vorobjeva and Obruchev (1964, fig. 17), but the differences between our interpretations of the Carboniferous and Permian forms are great. These authors have attempted to use a wide range of characters in the definition of the major taxa, e g, the degree of ossification of the endocranium, the structure of the dermal bones and scales, nature of the dentition and fins, as well as cranial roofing bone and mandibular dermal bone patterns. However, these characters are not consistently applied, mainly because of the inadequate preservation of many genera. Consequently many of the taxa seem to have arbitrary limits, and a large number of assignments of genera are acknowledged to be doubtful. One may take as an example the differences between their definitions of the suborders *Uronemoidei* and *Ctenodontoidei;* although "paired lateral occipitals" are listed for the *Uromemoidei* but not the *Ctenodontoidei,* and only the postsplenial and angular in the former and the postsplenial, splenial, and angular in the latter, are said to be fused, we can find no evidence to support discrimination on these bases (Watson and Gill, 1923; Westoll, 1949). The remaining differences listed refer to the degree of ossification of the endocranium and axial skeleton, the depth of burial of the lateral-line canals, and the dentition. These provide inadequate grounds for division at the subordinal level unless reinforced by strong phylogenetic arguments; such are not available.

Other problems arise, such as the separation of *Soederberghia* and *Fleurantia* into different families, but these are relatively minor.

Excluding those genera for which inadequate skull roofs are available, it can be seen that the classification of Romer (1966) produces groupings very similar to those outlined in our Figure 35. There are differences, as, for example, in the treatment of *Rhinodipterus* and *Pentlandia* and the relative status assigned to certain groups. The problem of *Rhinodipterus* has been discussed previously and need not detain us further. *Pentlandia* is, in our view, more closely allied to *Scaumenacia* than to *Dipterus,* and in Romer's classification should be assigned to the Phaneropleuridae. Finally, if the Uronemidae are to be separated from the Ctenodidae, and the Conchopomatidae from the Sagenodidae, as Romer suggests, the group *Phaneropleuron-Scaumenacia-Pentlandia* should be separated from that containing *Soederberghia-Jarvikia-Oervigia-Fleurantia-Rhinodipterus ulrichi,* even if subdivision of these groups is not carried further.

SUMMARY

Dipnorhynchus sussmilchi is shown to be an early Emsian-early Eifelian marine-dwelling dipnoan, adapted to feeding on shelly invertebrates or perhaps dead placoderms. Preparation of new material and of the holotype has shown that previous reconstructions have been in error because of the misinterpretation of the position of the infraorbital lateral-line canal and the consequent positioning of the orbit too far forward. A new reconstruction of the skull roof is given.

Using this reconstruction as a basis, and accepting the postulates that space capture rather than fusion offer the best basis for interpreting the dipnoan skull roof and that the bones on the posteromedian part of the skull provide the most stable points of reference, a series of definitions for the roofing bones is developed and applied to a representative series of Devonian and late Paleozoic genera. New features found in the roof of *Dipnorhynchus sussmilchi* are the complex division of the lateral-line system behind the orbit where there is a bone, T, not present in later genera; the complex D elements and the paired O elements; the probable existence of an H element between A and Z; the position of the occipital commissure on the loosely articulated elements Z-H-A; the absence of a rostral commissure; and the support of I by the dorsolateral crista of the braincase and of Y by the palatoquadrate.

The discovery of an isolated cheek plate carrying the lateral line canal and the determination of the position of the operculum from its attachment to the palatoquadrate have permitted the reconstruction of the cheek region, which is longer than that of all other known genera except *Uranolophus*. It is also more complex and contains many more bones.

The mandible of *D. sussmilchi* is a massive structure. The dermal bones can be readily compared with those of *Dipterus*. There is a long surangular extending from the articulation to the dentary, and similarly elongate angular, postsplenial and splenial. The prearticular is very robust and carries dental surfaces complementary to those of the palate. The dentary is well ossified and its dorsal surface extends back to make a long narrow dental ridge similar to a colinear ridge on the prearticular. In the curve of the dentary is a deep anterior furrow that may have contained sensory tissue in life. A large labial pit is present. The Meckelian bone is thick and strong and provides a surface for the attachment of the intermandibularis and geniocoracoideus muscles. It also forms a symphysial plate. Both mandibular and oral lateral-line canals are present, together with a mandibular commissure. The oral canal seems to terminate posteriorly within the surangular. Within the dentary there is a system of rostral tubuli of the same type as in the snout. A system of nerve and vascular canals can be readily distinguished and has been compared with those of *Neoceratodus*. Despite the obvious differences in size and dentition, and the length of the surangular, the basic structure of the mandible is shown to be essentially the same as that of *Dipterus*.

The palate of *D. sussmilchi* is a massive structure, lacking separate denticles and sutural indications of a separate parasphenoid element. The dental surface is marked by a series of massive rounded tuberosities that cannot be homologized with any structures in other Dipnoi. The palate is fused to the braincase without any indication of the original boundary between endocranial, palatal, and dermal components of the holostylic skull. The braincase is similarly fused to the dermal skull roof. The nasal capsules are large and the nares ventrally directed. The nasal organ was apparently subdivided into three separate recesses. The orbital and temporal chambers of the skull are delimited and partially separated by a curious dorsal process from the palate found elsewhere only in *Uranolophus*. The oticotemporal region of the braincase is covered laterally by the apposed massive palatoquadrate, forming an enclosed chamber around the trigeminofacialis nerve ganglion complex. Posterodorsally there is a massive adductor muscle chamber extending backward under the skull roof. Each chamber is subdivided by a dorsolateral crista of the braincase that rises to meet the underside of the skull roof; the chambers on either side are separated by a similar median crista. A similar arrangement is seen in *Chirodipterus* and *Dipterus* and the large adductor chamber is a common feature of all known Dipnoi.

A unique feature of the braincase of *D. sussmilchi* is that it included a unique otoquadrate bar, possibly homologous with the hyomandibula. In front of this is a deep recess, probably for a spiracular sense organ.

The scales and the fine structure of the dermal bones of *D. sussmilchi* are almost identical with those of *Uranolophus* and show marked similarity to those of Crossopterygii.

A new outline scheme for the evolution of the Paleozoic Dipnoi is presented. It depends primarily on dermal bone patterns of the head, but also takes into account such structures as the parasphenoid and the fins. It is our opinion that the new data on the hyomandibula, the cheek, the dermal bones of the mandible, and the scales provide strong evidence for the close relationship of the dipnoans and crossopterygians, and for the sarcopterygian concept of Romer.

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FIGURES 36–95

Figs. 36–39. The skull of *Dipnorhynchus sussmilchi.*

36. Specimen 18815, Australian National University. Dorsal view. ×.77.
37. Anterior view of same specimen as Figure 36. × .95.
38. Holotype. Dorsal view. ×.77.
39. Anterior view of same specimen as Figure 38. ×.95.

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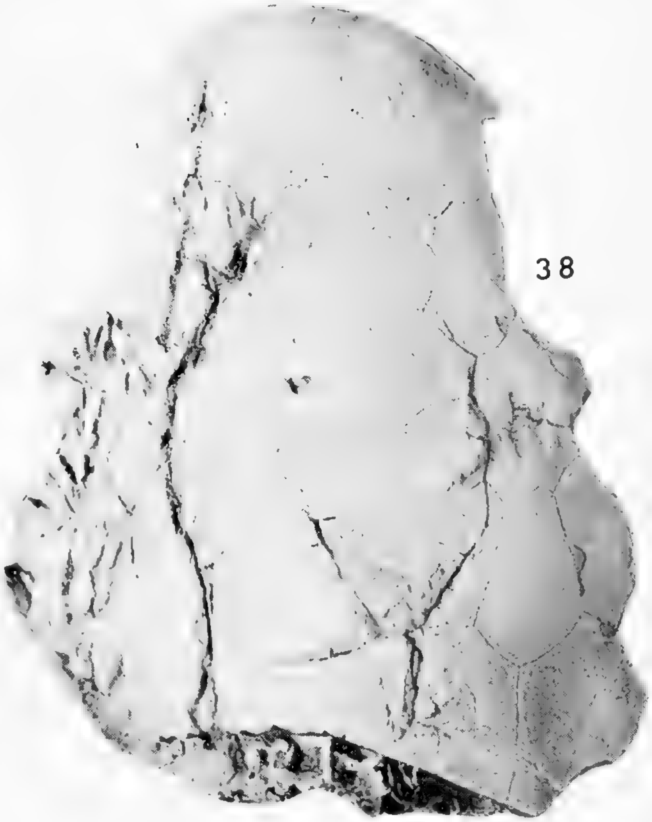

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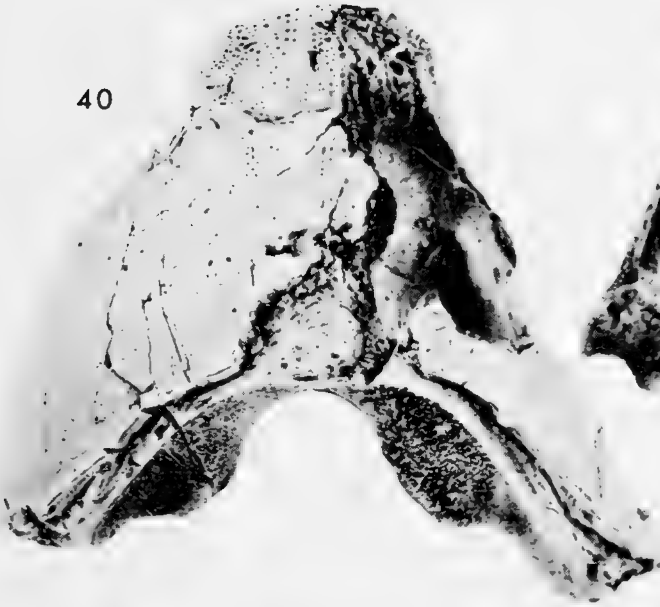
Figs. 40–45. *Dipnorhynchus sussmilchi.* Mandible, specimen P 46773, British Museum (Natural History).

40. Mandibles in ventral view. ×1.0.
41. Mandibles in dorsal view. ×1.0.
42. View toward the anterior along the Meckelian vacuity of the right ramus, prearticular and Meckelian bone on the left, postsplenial and part of the articular at the bottom. Note the furrows across the latter bones, the left one leading to the foramen in the anterior furrow and the right to a foramen opening into the rostral tubuli. ×1.5.
43. Posteroventral view of mandibles. ×1.0.
44. Right mandible in lateral view. ×1.0.
45. Left mandible in lateral (and slightly anterior) view. ×1.0.



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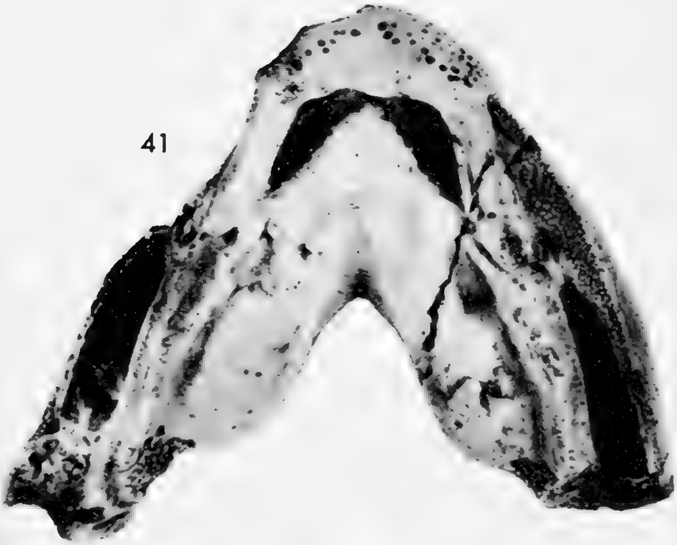

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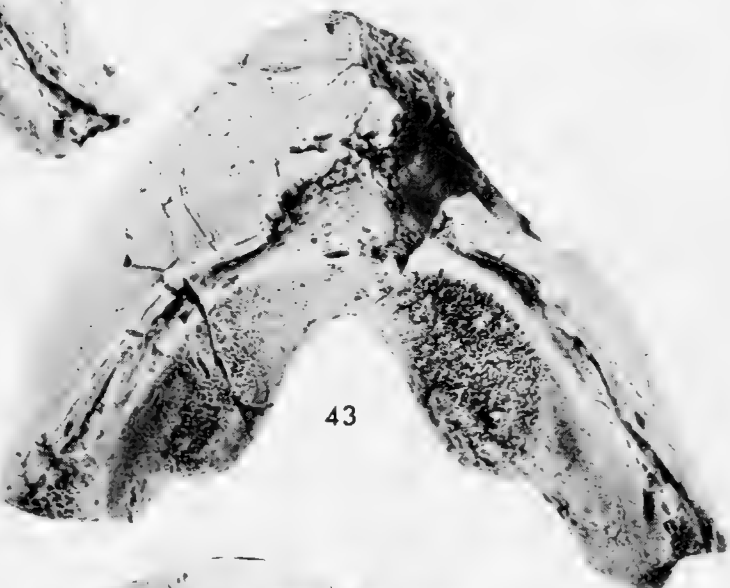

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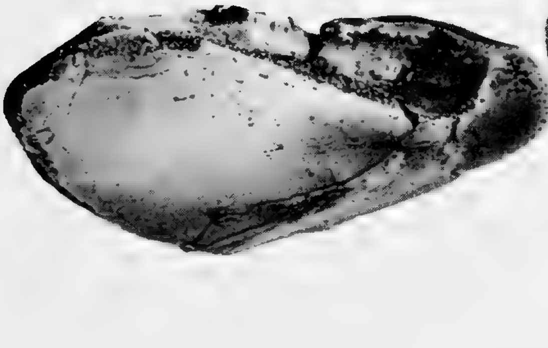

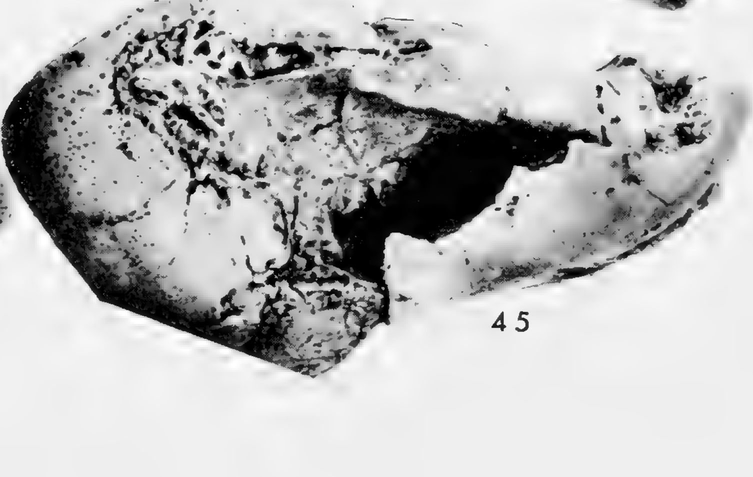

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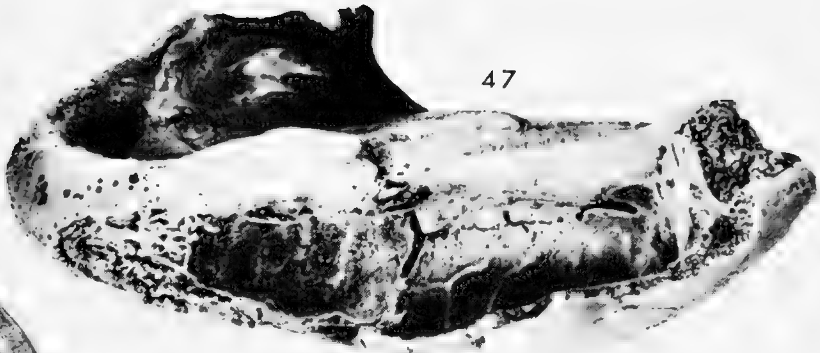
Figs. 46–50. *Dipnorhynchus sussmilchi.* Mandible. Figs. 46–47, same specimen as Figs. 40–45. Figs. 48–50, specimen P 13837, National Museum, Melbourne.

46. Mandible in dorsal view. ×0.75. (Specimen, not whitened, showing well the deep median groove.)
47. Left mandible in lateral (and slightly dorsal) view, showing the Meckelian vacuity. ×1.1.
48. Left mandible in lateral view showing the vertical ridges in the medial wall of the Meckelian vacuity. ×0.85.
49. Right mandible in ventral view, showing the Meckelian vacuity. ×0.85.
50. Mandibles in dorsal view. ×0.75.

47



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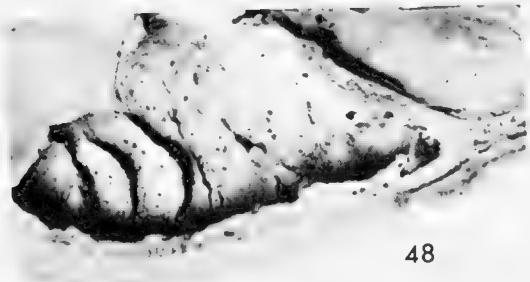

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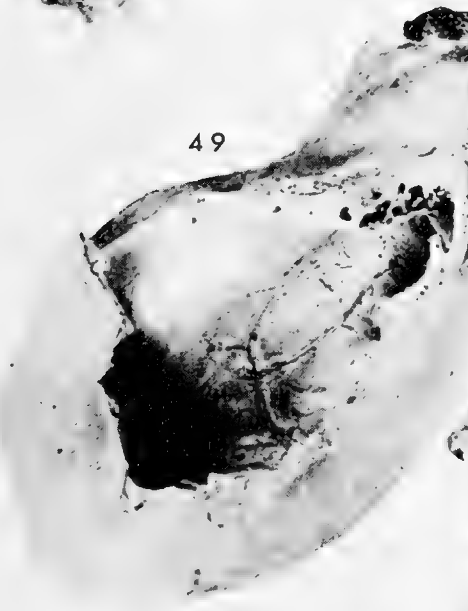

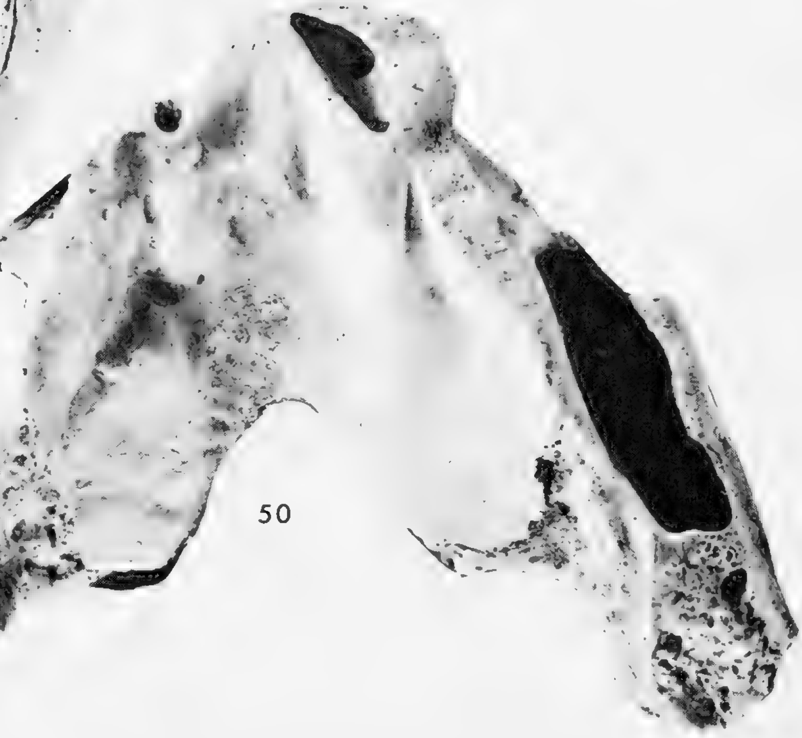

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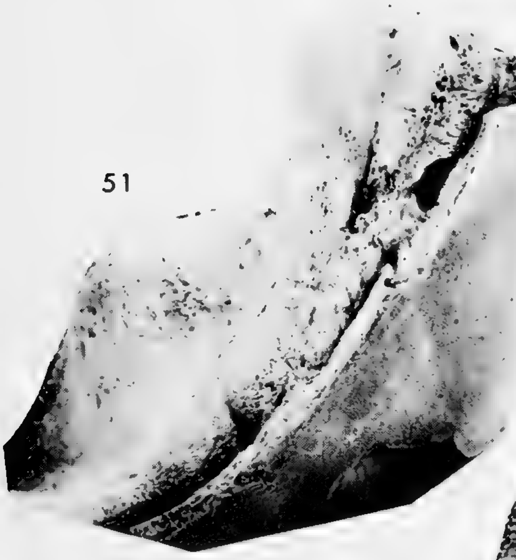
Figs. 51–54. *Dipnorhynchus sussmilchi.* Mandible, same specimen as in Figs. 48–50.

51. Posteroventral view of posterior end of right ramus. ×0.9.
52. Ventral view of right ramus. ×0.9.
53. Posterior view of mandibles. ×0.75.
54. Anterior view of mandibles. ×0.75.

51



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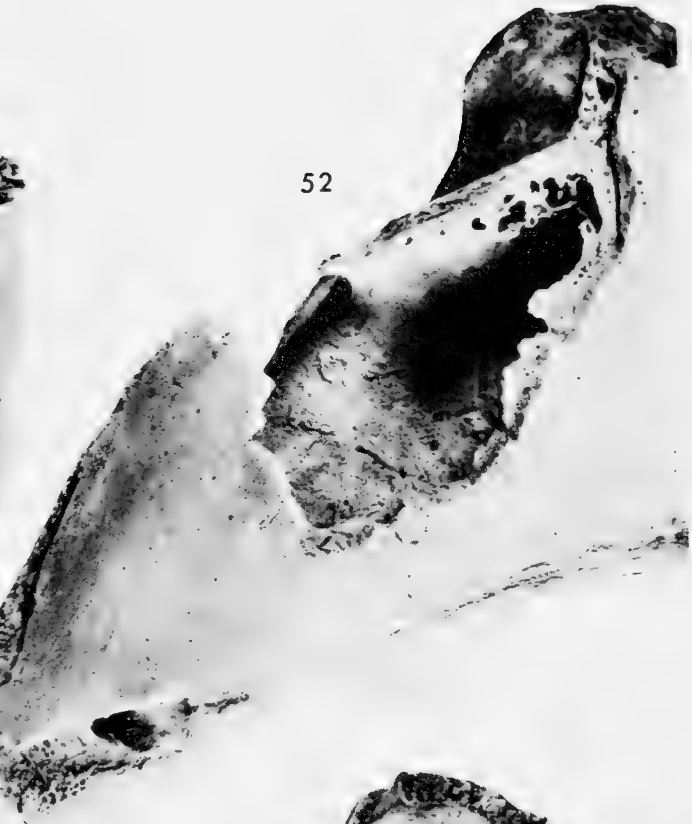

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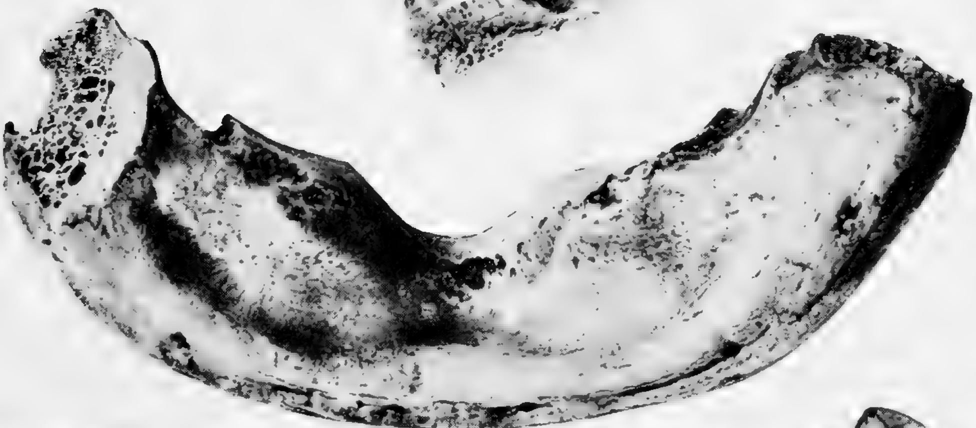

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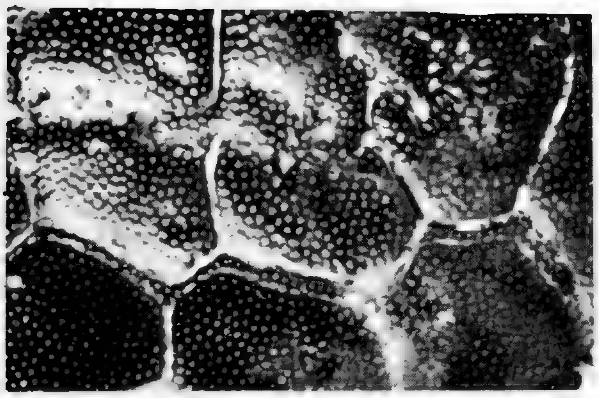
Figs. 55–62. *Dipnorhynchus sussmilchi.*

55. Detail of dermal bone surface in rostral region. Specimen 18815, Australian National University. ×5.5.
56. Detail of bone structure on the upper posterior surface of the dentary. Photographed under alcohol. Specimen P 33714, British Museum (Natural History). ×42.
57. Detail of bone structure on rostral part of dentary; large pores open into rostral tubuli. Photographed under alcohol. Same specimen as Fig. 56. ×21.
58. Detail of surface of postsplenial showing cosmine. Surface oiled. Same specimen as Fig. 56. ×21.
59. Detail of surface of right surangular. Specimen P 33714, British Museum (Natural History). ×1.4.
60. Detail of posterior end of right mandibular ramus. Posteroventral view. Same specimen as Fig. 59. ×1.4.
61. Detail of dorsal surface, posterior end of right jaw ramus. Same specimen as Figs. 59 and 60. ×1.4.
62. Ventrolateral view of broken edge of left dentary showing the rostral tubuli, the ragged edge of the enamel surface of the dentary overlapping the spongy bone of the inner wall of the labial pit, and the canal system on the medial wall of the Meckelian vacuity. Specimen P 46773, British Museum (Natural History). ×1.4.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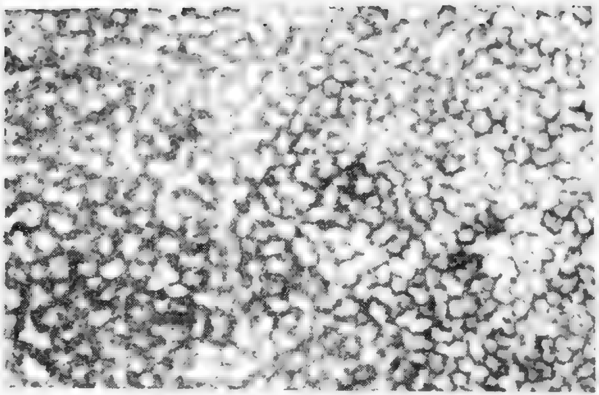
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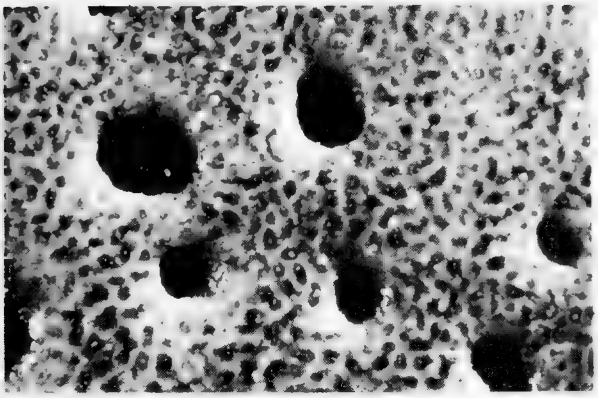
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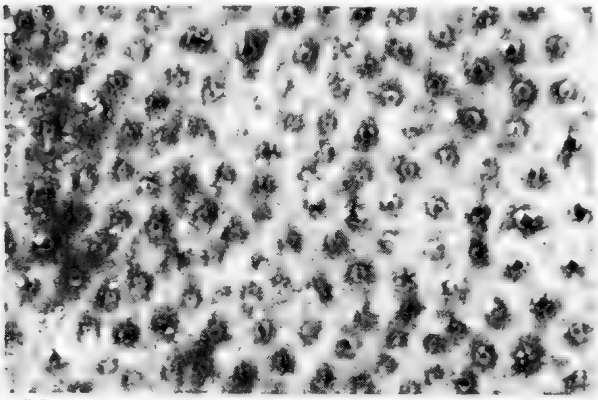
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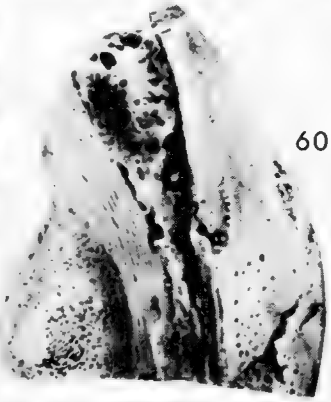
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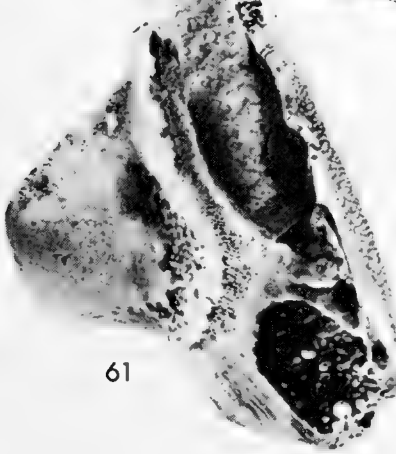
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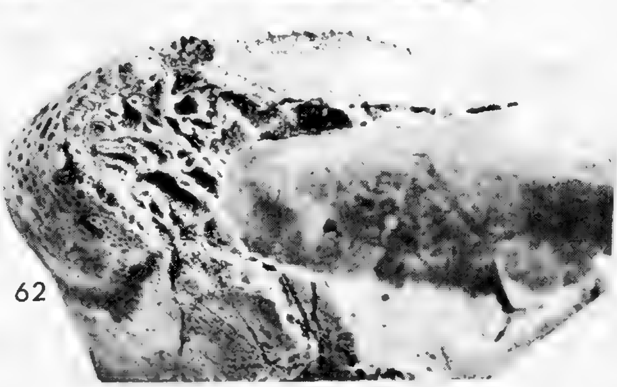
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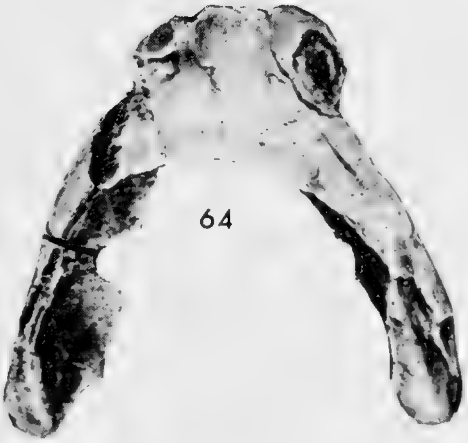
Figs. 63–68. *Dipterus valenciennesi.* Mandible, specimen 53377, Geological Survey, London (Figs. 63–67). Palate, specimen 1859.33.612, Royal Scottish Museum, Edinburgh (Fig. 68).

63. Ventromedial view of left mandibular ramus. ×1.5.
64. Ventral view of mandibles. ×1.1.
65. Ventral view of left ramus. ×1.5.
66. Lateral view of left ramus. ×1.5.
67. Cross section through right mandibular ramus, seen in anterior view. ×3.0.
68. Palate, incomplete; ventral-surfaced solum nasi eroded showing vascular canals within. ×0.75.

63



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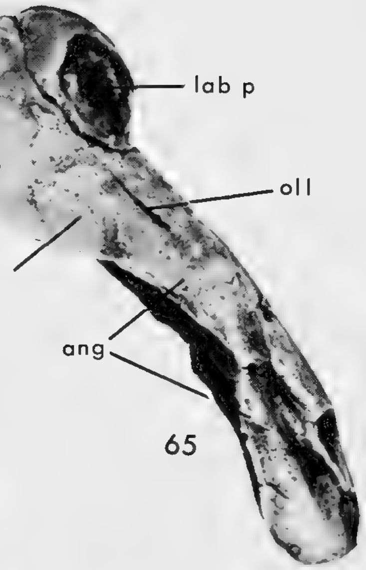

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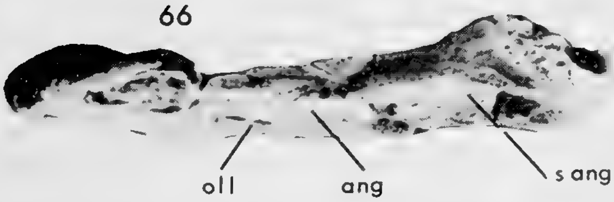

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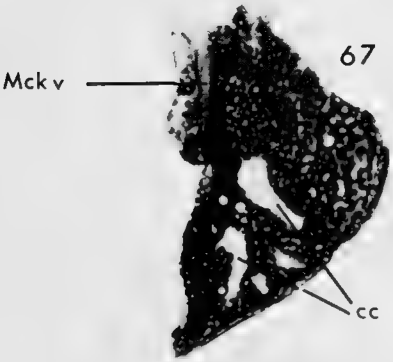

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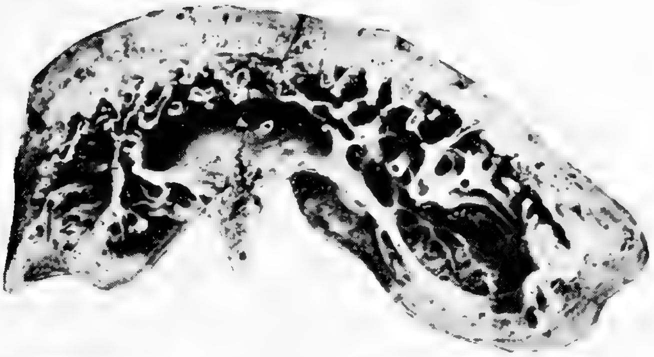
Figs. 69–73. *Dipnorhynchus sussmilchi.* Palate. Specimen 33699, British Museum (Natural History).

69. Detail of portion of snout region broken through naturally, showing the rostral tubuli. Dorsal view. ×0.95.
70. and 71. Portion of the snout and incomplete palate, in ventral view. Natural association. ×0.8.
72. and 73. Portion of the snout and incomplete palate, in dorsal view. Natural association. ×0.8.

69



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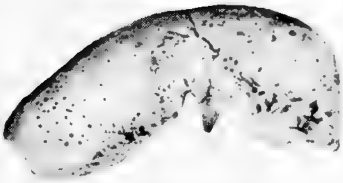

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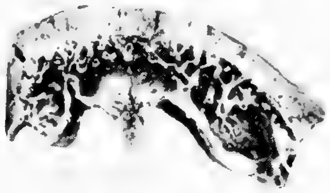

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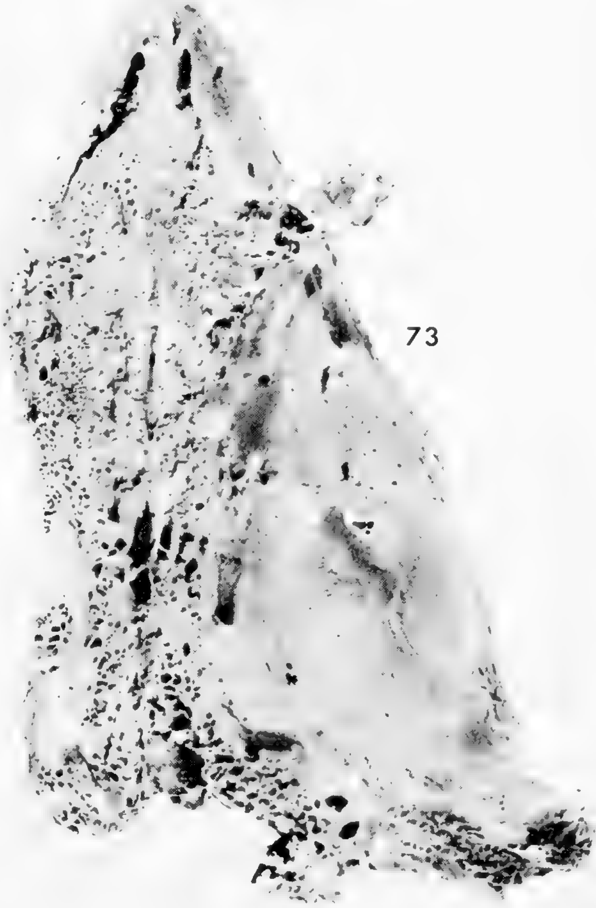

Figs. 74–77. *Dipnorhynchus sussmilchi.* Braincase and palate.

74. Ventral view of skull. Specimen 18815, Australian National University. ×0.8.
75. Ventral view of skull. Holotype. ×0.8.
76. Posterior view of skull, same specimen as Fig. 74. ×0.85.
77. Detail of quadrate region of the palate. Same specimen as Fig. 75. ×1.1.

74

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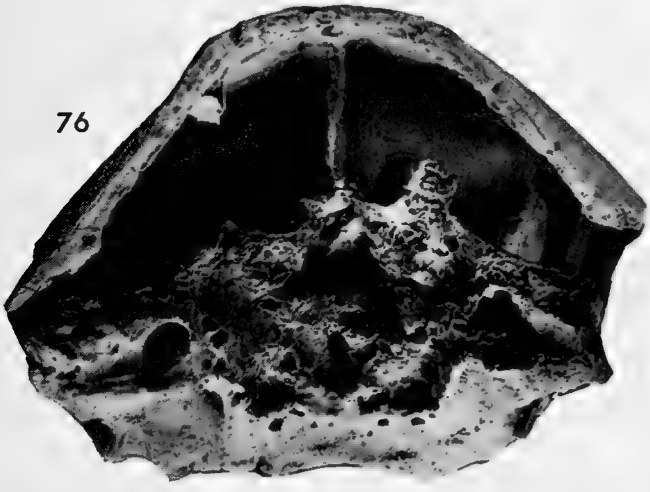

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Figs. 78–81. *Dipnorhynchus sussmilchi.* Skull and lower jaws.

78. Skull in right ventrolateral view, showing lateral wall of braincase. ×0.75.
79. Anterior portion of skull in left lateral view showing the small rounded irregular tubercles along the palate margin. Specimen 18815, Australian National University. ×0.8.
80. Mandibles in lateral (and slightly dorsal) view. Specimen P 46773, British Museum (Natural History). ×1.1.
81. Skull in right lateral view, showing ventral portion of lateral wall of braincase. Same specimen as Fig. 78. ×0.75.

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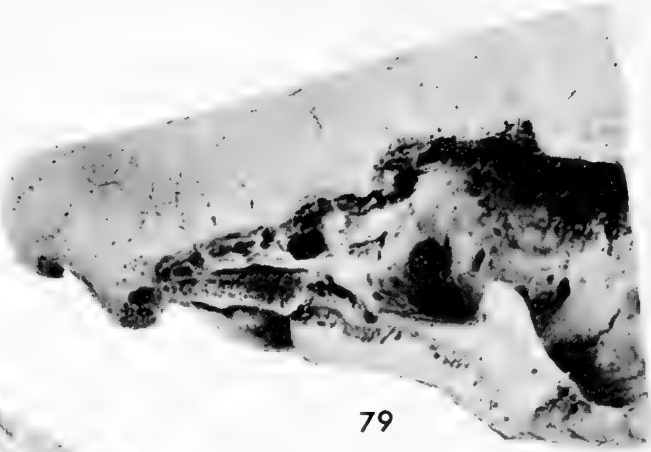

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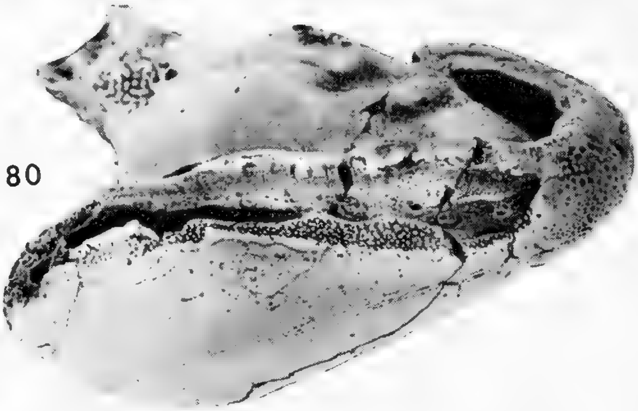

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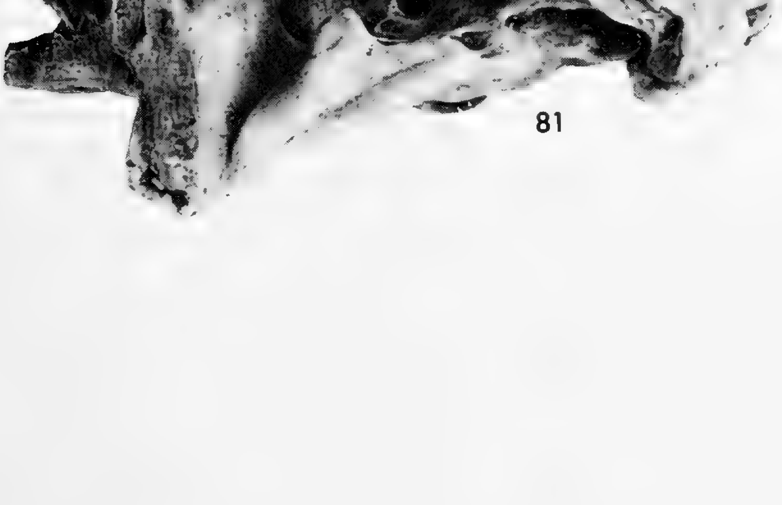

Figs. 82–85. *Dipnorhynchus sussmilchi.* Braincase.

82. Posterior view of braincase. Holotype. ×0.7.
83. Detail of the region of the jugular canal. Holotype, same posterior view as Fig. 82. ×1.1.
84. Posteroventral view of posterior region of the skull. Holotype. ×0.7.
85. Posteroventral view of the posterior region of specimen 18815, Australian National University. ×0.8.

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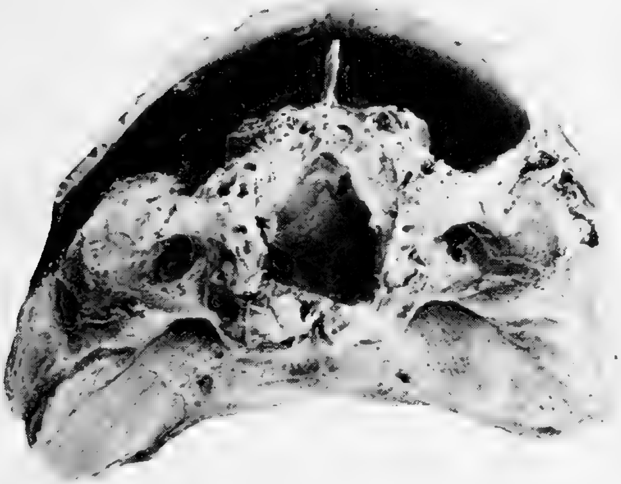

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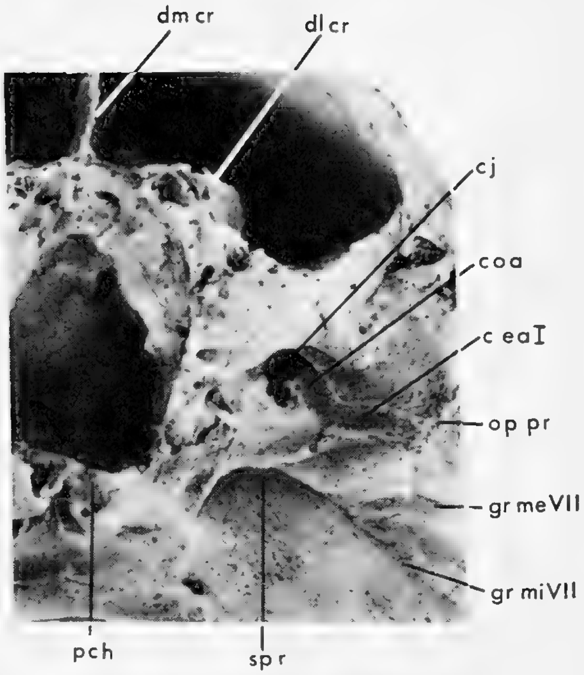

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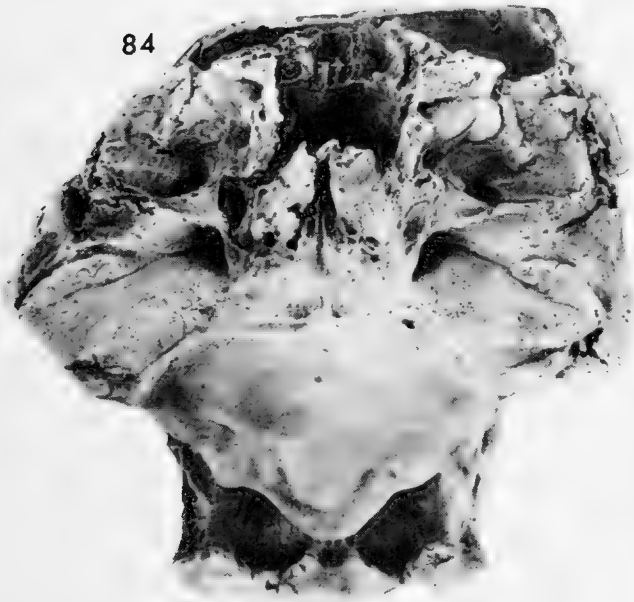

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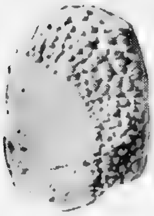
Figs. 86–91. *Dipnorhynchus sussmilchi.* Scales, branchial element and cheek element.

86. Scale in (a) lateral and (b) medial view. P 13837B, National Museum, Melbourne. ×1.6.
87. Two scales in medial view.
    (a) P 13837C, National Museum, Melbourne. ×1.6.
    (b) P 13837F, National Museum, Melbourne. ×1.6.
88. Scale in (a) lateral and (b) medial view. P 13837D, National Museum, Melbourne. ×1.6.
89. Scale in (a) lateral and (b) medial view. Portion of Holotype (F 10813B), Australian Museum, Sydney. This was originally described as part of the palatal ornamentation; see text. ×1.6.
90. Portion of hypobranchial skeleton in (a) ventral, (b) right lateral, and (c) dorsal view. P 13837G, National Museum, Melbourne. ×1.6.
91. Isolated element 8 from right cheek in (a) posterior, (b) lateral, and (c) medial view. Specimen P 13837A, National Museum, Melbourne. ×1.2.

86a



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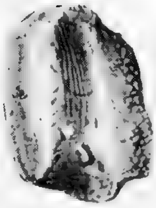

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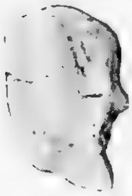


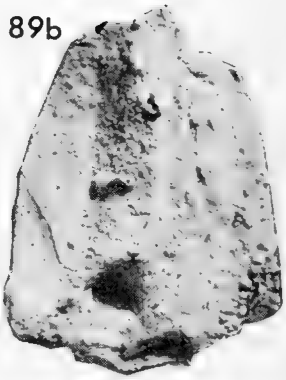
87b

88a

88b

89a

89b



90b

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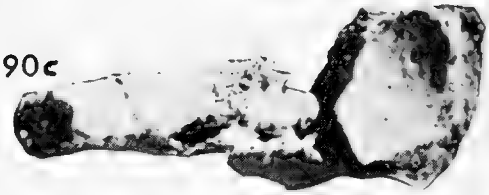
90c



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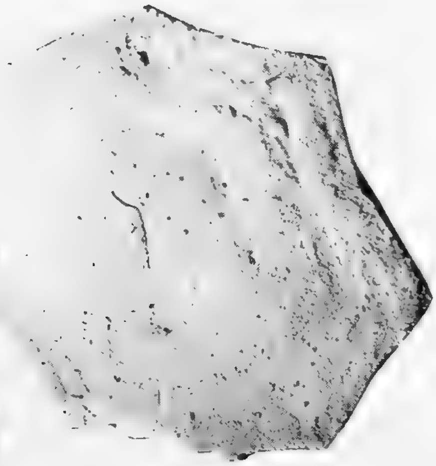

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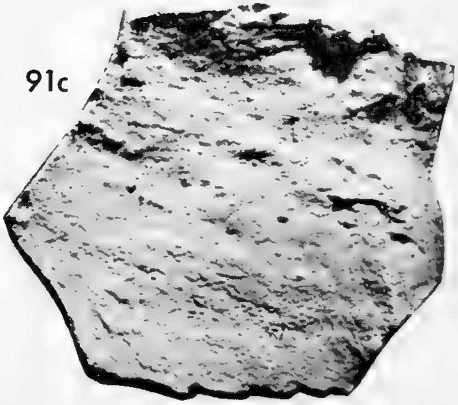
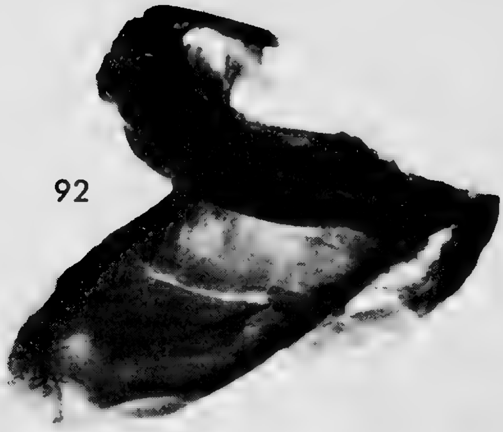


91a

Figs. 92–95. *Dipnorhynchus sussmilchi*. Mandibles, palate, and cheek.

92. Mandibles in ventrolateral (and slightly posterior) view as seen by X ray. The X-ray beam is perpendicular to the axis of the left mandibular ramus. Specimen P 46773, British Museum (Natural History). ×0.8.
93. Mandibles in ventral view, as seen in X ray. Same specimen as Fig. 92. ×0.8.
94. Palate in dorsal view, as seen in X ray. Specimen P 33699, British Museum (Natural History). ×0.8.
95. Element 8 from right cheek, as seen in X ray. Specimen P 13837A, National Museum, Melbourne. ×0.8.



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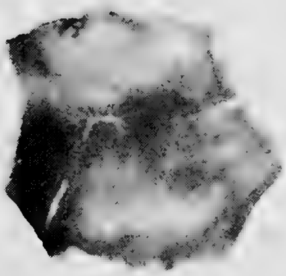

95

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