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An Advanced Massive Dipnorhynchid Lungfish
from the Early Devonian of New South Wales, Australia

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ABSTRACT. *Dipnorhynchus kurikae* is a large dipnoan of Zlichovian age from limestones at Wee Jasper, New South Wales. Its skull roof is very broad posteriorly, narrow rostrally, has a pineal foramen opening through a single 'D' bone and a small number of bones in front of 'D'. The palatal and mandibular tooth plates are massive. The species is a close relative of *D. sussmilchi*.

Several highly significant fossils were found closely associated in the Zlichovian Limestones at Wee Jasper, New South Wales (Fig. 1). Among these were a partial skull roof, palate and mandible of a massive dipnoan. Subsequently another fragment of a skull roof and two partial palates were recovered from the same locality. A similar large mandible had been found at this locality several years previously but it had been regarded as a gerontic individual of *Dipnorhynchus sussmilchi* (Campbell & Barwick, 1983). The skull fragments and three palatal fragments, which are all of comparable dimensions, provide enough data to demonstrate that a more advanced form than *D. sussmilchi* is represented. Using the criteria usually applied in the differentiation of genera and species of Devonian Dipnoi, this material is described as a new species.

SYSTEMATIC PALAEONTOLOGY

Dipnorhynchus kurikae n. sp.

Figs 2–10

The holotype is ANU35674, the posterior part of a skull roof; paratypes ANU35675, 36508–36510 and 36519 are a partial skull roof, three partial palates and a snout respectively; ANU35643 and AMF64832 are partial mandibles. All come from the shore of Burrinjuck Dam, Goodradigbee River (Fig. 1).

The species is named in honour of Dr Elga Mark-Kurik who discovered the first skull roof fragment.

Formation and Age. From the transition between the Bloomfield and *Receptaculites* Limestones, Goodradigbee River, Wee Jasper, N.S.W. One of the specimens occurs about 10 m higher in the section than the others, and is within the *Receptaculites* Limestone. Zlichovian.

Diagnosis. Large species. Width to length ratio of skull high, this ratio for the palate being ca. 1.5. Large 'K' not extending between 'X' and 'L'. 'I' bones meeting behind 'B'. Pineal foramen open. One to three 'D' bones present. One to three 'L' bones depending on size of 'K'. Bones 'M' and 'N' large. Rostrum narrow. Palate exceptionally thick and transverse across the articular region. Small anterior median palatal bone embraced within paired 'dermopalatines', and all fused to the pterygoids. Dentition consisting of bulbous masses similar to those of *D. sussmilchi*. Dentine thin over most of the palate but thicker on the marginal ridges and the bulbous 'teeth'. Mandible very long medially and with a very powerful symphysis; ratio of median length/total length ca. 0.70. Anterior furrow deep, and divided by a forward extension of the 'adsymphysial' plate, at least in large adults. 'Dentary' very short on the ventral side of the mandible but with long dorsolateral extensions around the anterior furrow. 'Splenials' and 'postsplenials' long and narrow. 'Surangular' deep and long, extending forwards to the anterior end of the labial pit. Massive bulbous tuberosities on the heel of the 'prearticulars' and smaller elongate teeth immediately behind the anterior furrow. Marginal ridge on the dentary continuous with that on the anterior end of the 'prearticulars'. Dentine thicker on the marginal ridges and bulbous teeth than elsewhere.
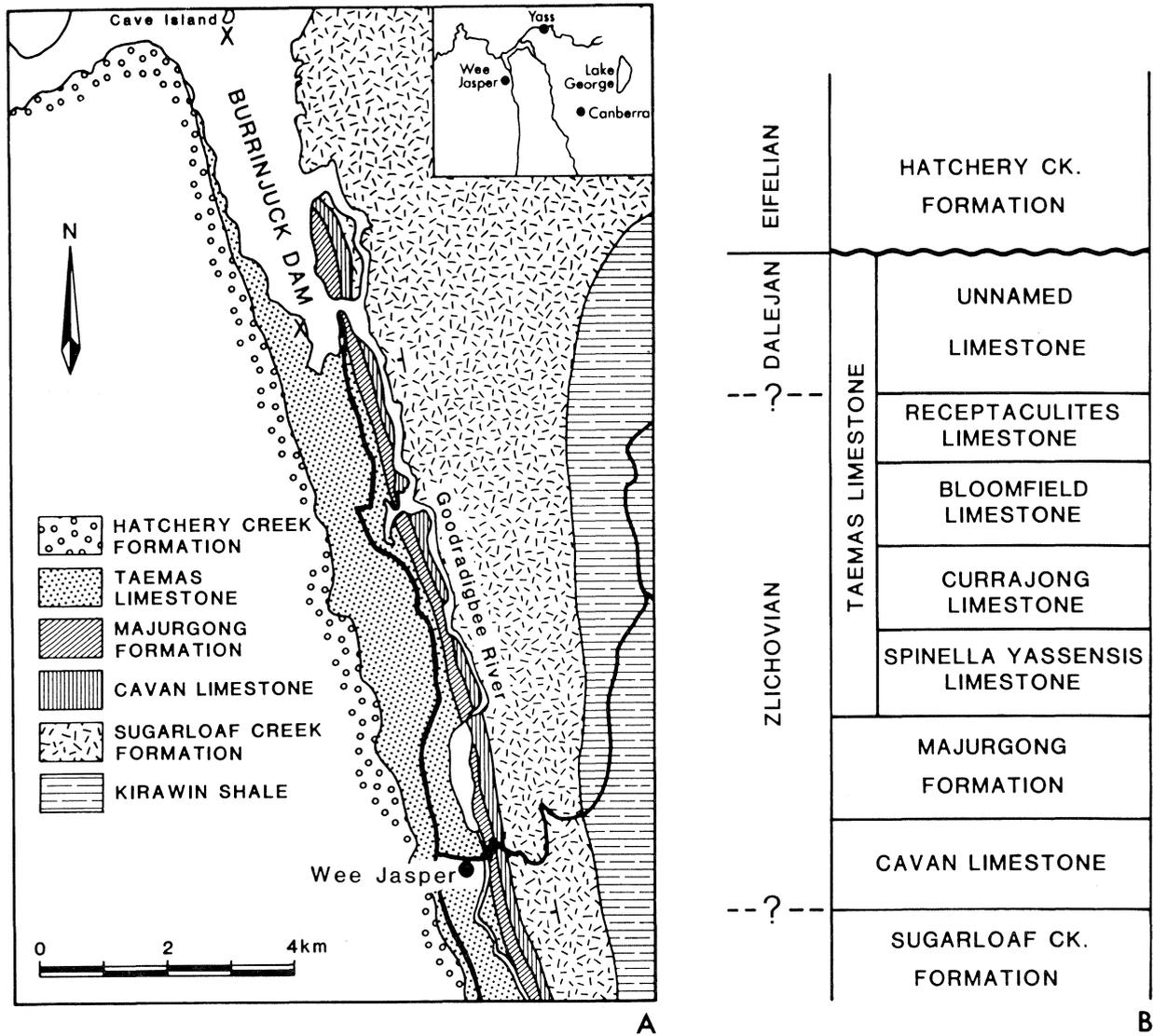
Fig. 1. a, Geological map of the Wee Jasper area, N.S.W. Main collection site marked X; b, subdivisions of the Taemas Formation in the Wee Jasper area.

Comparative Description. The large 'D' with the open pineal foramen in the holotype is unlike the arrangement seen in any other known genus. *Uranolophus wyomingensis* has a comparably large 'D' but no pineal foramen. The paratype ANU35675, with its second and perhaps third 'D' bone, is more like *D. sussmilchi*. The reduction of the number of 'D' bones is a well known feature of dipnoan evolution (Miles, 1977, p.305), and it is clear that *D. kurikae* has advanced well beyond the *sussmilchi* stage in this character.

Bone 'K' is in the primitive position relative to 'X' and 'C', but it is very variable in size. In ANU35675 it is comparable in size with the bone 'K' in *D. sussmilchi*, but in the holotype it is greatly expanded, particularly on the left side where it occupies the space

of bone 'L$_1$' as well as 'K'. In this respect it should be noticed that the type of *Speonesydrion lehmanni* (Campbell & Barwick, 1984b) and some variants of *Uranolophus wyomingensis* have a comparably large bone in this position (Denison, 1968, fig. 3).

The lateral line canal from 'J' passes directly to 'K' and the radiographs of ANU35675 show no signs of an anastomosis with the canal in 'X'. Bone 'X' is massive, and proportionately wider than the equivalent in any other species. Bone 'L$_2$' also is unusually large, and on the left side of the holotype it is enormous. The 'I' bones are very transverse and their ossification centres are posteriorly placed.

Part of a snout has already been illustrated (Campbell & Barwick, 1984a, fig. 6). This is well ossified and has
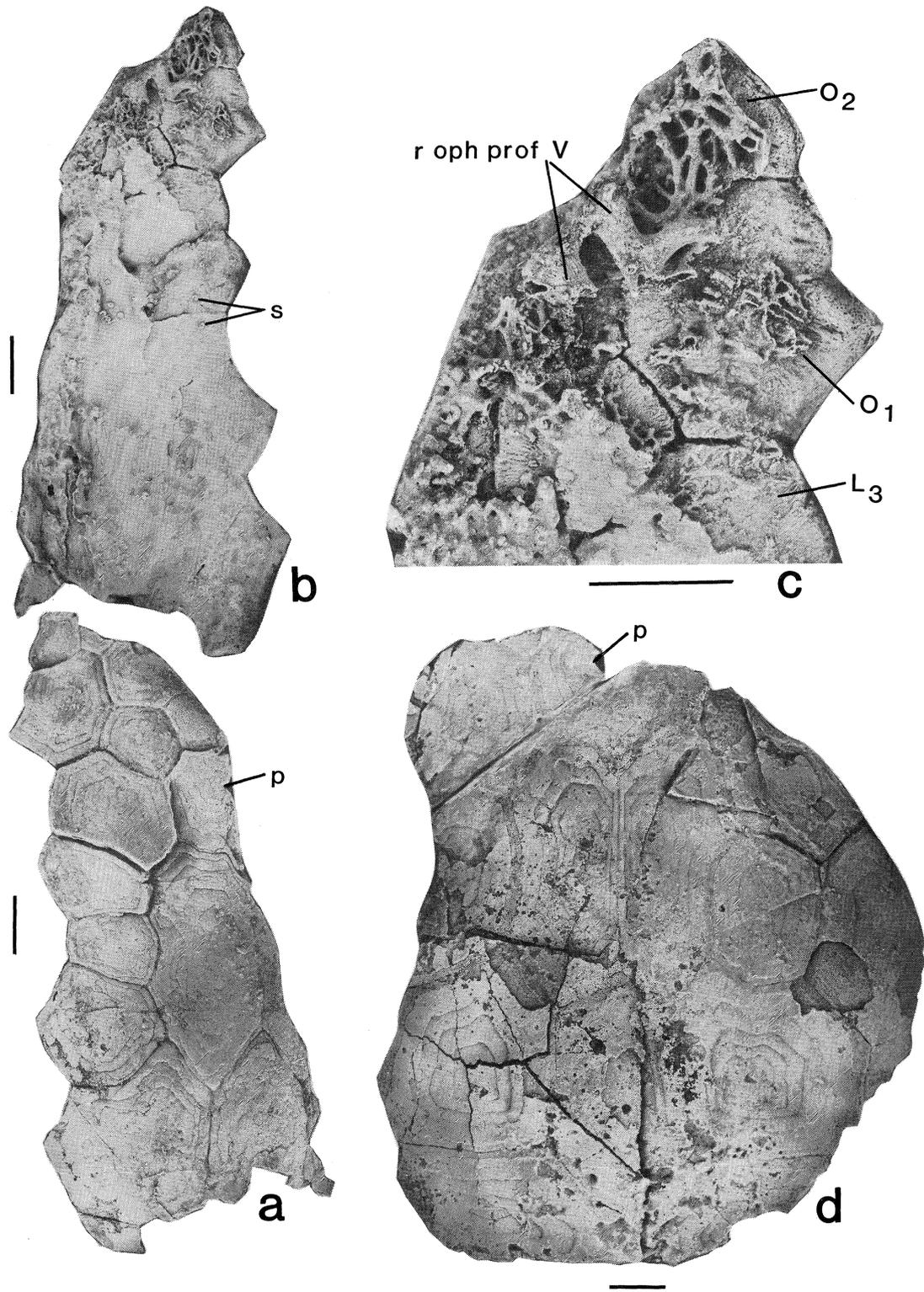
Fig. 2. a, b, Skull roof of ANU35675 in dorsal and ventral views respectively. The specimen is slightly humped and twisted medially as a result of tectonic distortion; c, enlargement of the canals in the ethmoid capsule of the same specimen; d, the holotype roof. p = pineal foramen; r oph prof V = ramus ophthalmicus profundus V; s = encrusting serpulid worms; L_3, O_1, O_2 = dermal roofing bones. Scales = 10 mm.
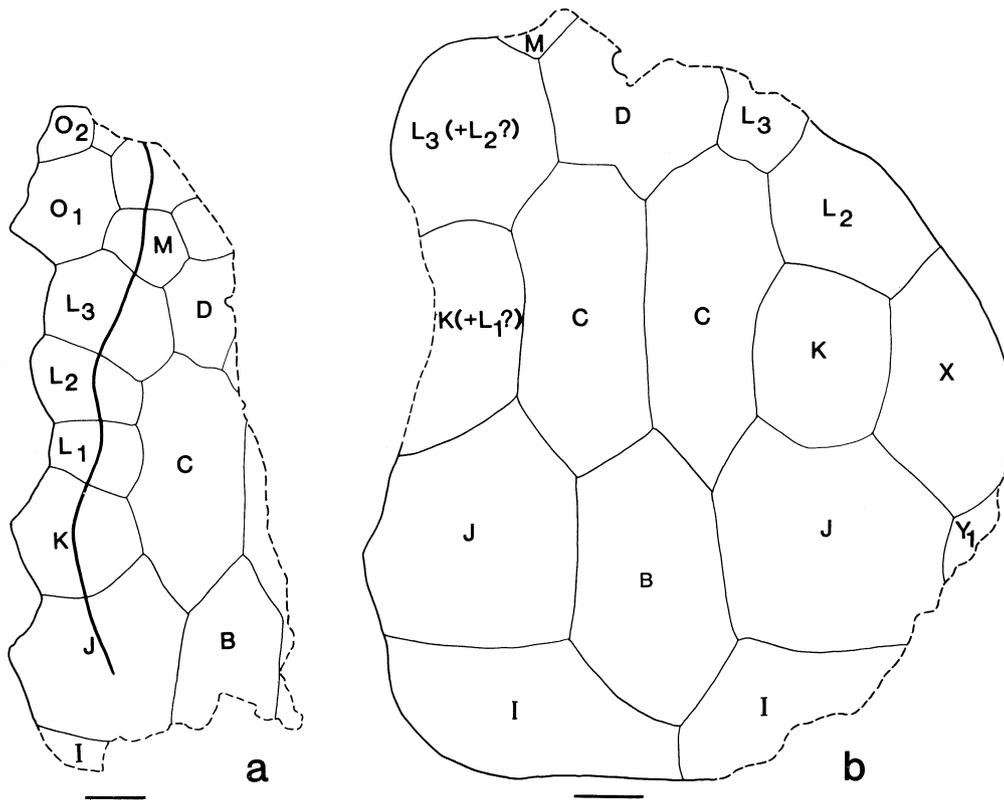
Fig. 3. Interpretation of the two skull roofs shown in Figure 2. The lateral line canals in ANU 35675 have been located from X-radiographs. Scales = 10 mm.

numerous perforations associated with the lateral line and rostral tubule systems. It also is a narrow structure, which makes it easy to distinguish from the much broader snouted *Speonesydrion iani* with which it occurs.

The number of bones anterior to 'D' cannot be determined from the available specimens, but judging from ANU35675 in which the single large 'N' extends well towards the mid-line and the bone immediately in front of 'D' is large, the number of bones must be less than in *D. sussmilchi* and *D. kiandrensis*. Bone '3' must have been very large on the fragment ANU35675, as is shown on the reconstruction on the left side of Figure 4. There it is in contact with 'K', an unusual feature which is also found on one side of the holotype of *D. sussmilchi*. Thus the skull roof shows a mixture of advanced and primitive characters.

A few tubules from the ethmoid capsule are preserved under the rostral region of ANU35675. Two very large interconnected tubes are present medially. From their position relative to the lateral line canal and the roofing bones, they can be homologised with canals connected with the medial and lateral branches of the profundus nerve. A fragment of what is probably part of the superficial ophthalmic canal is present marginally. All these tubules are interconnected and they ramify towards the dermal bones as described previously in *D. kiandrensis*.

The palate is reminiscent of *D. sussmilchi* in overall shape and in the presence of bulbous tuberosities. These become disproportionately massive in large specimens. There is a median tuberosity at the anterior end of each pterygoid and this was probably contiguous with a smaller tuberosity on the anterior median plate, as in *D. sussmilchi*. The marginal ridge is weakest posteriorly and extends forwards to the anterior end of the pterygoid where it forms a semi-isolated elongate 'tooth'. Posterolaterally on each pterygoid there is a broad concave surface that occludes with the main tuberosities on the mandible. Between these surfaces on the smaller specimens is a flat low eminence, but on the largest individual, ANU36510, the eminence is massive and transverse. This leaves a deeply concave medial surface on the palate as a whole (Fig. 5). The dentine is thin over the concave surfaces but more than doubles its thickness on the tuberosities (Fig. 6). Nevertheless it is clear that the prominences on the palate are largely formed of bone with relatively thin dentine surfaces.

The dentine is not well preserved, but on the tuberosities it is of the same type as that found on the heels of the tooth plates in *Speonesydrion* (Campbell & Barwick, 1983, fig. 12). On all four specimens of the palate available, the dentine on the flat or concave surfaces consists of two distinct layers. The outer layer is less than 1 mm thick and consists of heavily mineralised tissue with almost completely occluded pulp

canals. It cracked easily during preservation, and while being prepared it tended to peel away cleanly from the underlying tissue. This consists of uniform vertical pulp canals ca. 0.07–0.12 mm in diameter, and is clearly distinguished from the underlying coarser bone. The preservation does not permit the recognition of circumpulpal or interstitial dentine if such were present.

Cross sections at various positions through the palate show no sign of sutures between the pterygoids or between the pterygoids and the parasphenoid. However, the dermal palatal bones thicken considerably towards the mid-line where they form a pronounced ridge supporting the base of the neurocranium (Fig. 6d). This same figure clearly shows the extent of the neurocranium on the floor of the anterior part of the orbital chamber, the boundary between the dermal and neurocranial bone being very sharply defined. The extent of the canal system traversing the neurocranial bone is also well seen (cf. Campbell & Barwick, 1982a, fig. 16; 1984b, fig. 9B, for similar structures in *D. sussmilchi* and *S. iani*).

The hypophysial stalk is long and thin (Fig. 6e) and opens through a small foramen near the posterior end of the palate. It is inclined at an angle of ca. 40° to the palatal surface. The palatine nerves and arteries leave the hypophysial pit in the same manner as in other Early Devonian dipnoans.

As in all these primitive genera in which dentine covers the whole palatal surface, the limits of the parasphenoid on the palatal surface cannot be observed, but it is assumed that the hypophysial stalk lay approximately parallel to the anterior edge of the parasphenoid as it does in *Chirodipterus australis* (see Campbell & Barwick, 1982a, figs 6a–d). Cross sections do not show any sign of a suture between the parasphenoid and the pterygoids, but the bone structure of the parasphenoid is coarser than that of the pterygoids (see Fig. 6c, e). The posterior face of ANU36508 shows the coarsely vesicular bone of the parasphenoid, and the distinctive structure of the bone that lies immediately beneath the dentine covering its ventral surface (see below). The posterior part of the parasphenoid is not preserved completely but what there is of it resembles the equivalent part of *D. sussmilchi*.

The quadrate is a massive bone and stands almost vertically. Its front wall is heavily dimpled, presumably for the attachment of muscles. On ANU36510 the whole of the unfinished surface occupied by the articulatory cartilage pad in life, is beautifully preserved. The cartilage must have been extremely thick, and acted as a resilient stress-bearing tissue to resist the forces of the massive bite. Its outline clearly shows a narrowing and slight protrusion of the lateral part of the surface to match the form of the glenoid fossa.

On the medial side of the articulatory surface is an enormous striated area for the attachment of the pterygoid-mandibular ligament. This is so large a structure that the pterygoid has developed a special process to carry it in ANU36510 the largest specimen, though in ANU36509 no such process is present.
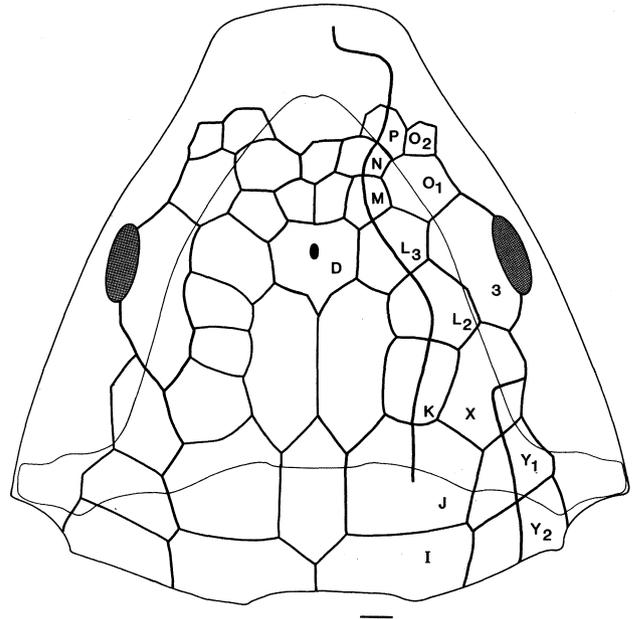
Fig. 4. Reconstruction of a dorsal view of the skull of *Dipnorhynchus kurikae* with the outline of a palate beneath. The left side of the roof is modelled on ANU35675 and the right side on the holotype. A single bone 'D' is figured as in the holotype. The roof anterolateral to 'D' is known only on the former specimen, and hence the right side reflects that same individual. Bone 'P' has been restored from the preserved fragment and the location of its centre fixed by projecting the lateral line canal in 'N'. Bones '3' are outlined from what is known of their inner edges, and the postion of the orbits in *D. sussmilchi*. The sizes of bones 'Y$_1$' and 'Y$_2$' are inferred from a restoration of the skull width by superimposing the outline of the palate on the roofing pattern; they could be somewhat wider than shown. The width of the snout is inferred from a single fragment, the position of 0$_1$ and 0$_2$, which limits the width in that region, and the superposition of a mandible, the dentary of which should fit neatly between the ends of the subnasal ridges. No attempt has been made to restore the cheeks. Scale = 10 mm.

In the angle between the parasphenoid and the pterygoid is a deep triangular pyramidal pit, similar to that described for *D. sussmilchi* (see Figs 5c, 7). Specimen ANU36510 is so large, and the foramina associated with this pit are so clear, that it is possible to clarify some of the points related to this structure. It has three canals leading into it from the posterior, two into its apex and the other into its ventromedial side. Of the two opening into the apex, the more lateral one is a continuation of a groove across the posterior face of the quadrate, running off that bone behind the jaw articulation. A similar groove occurs in *D. sussmilchi* where it has been interpreted as the r. mentalis externus VII. The more medial of the two apical openings connects with a groove that runs around the edge of the parasphenoid, and is interpreted as being for the internal carotid artery. The third (medial) opening is also connected with this groove. The canal into which the foramen opens cannot be traced with certainty, but it has an anterodorsomedial orientation. At present it can be identified only as a branch of the internal carotid artery.
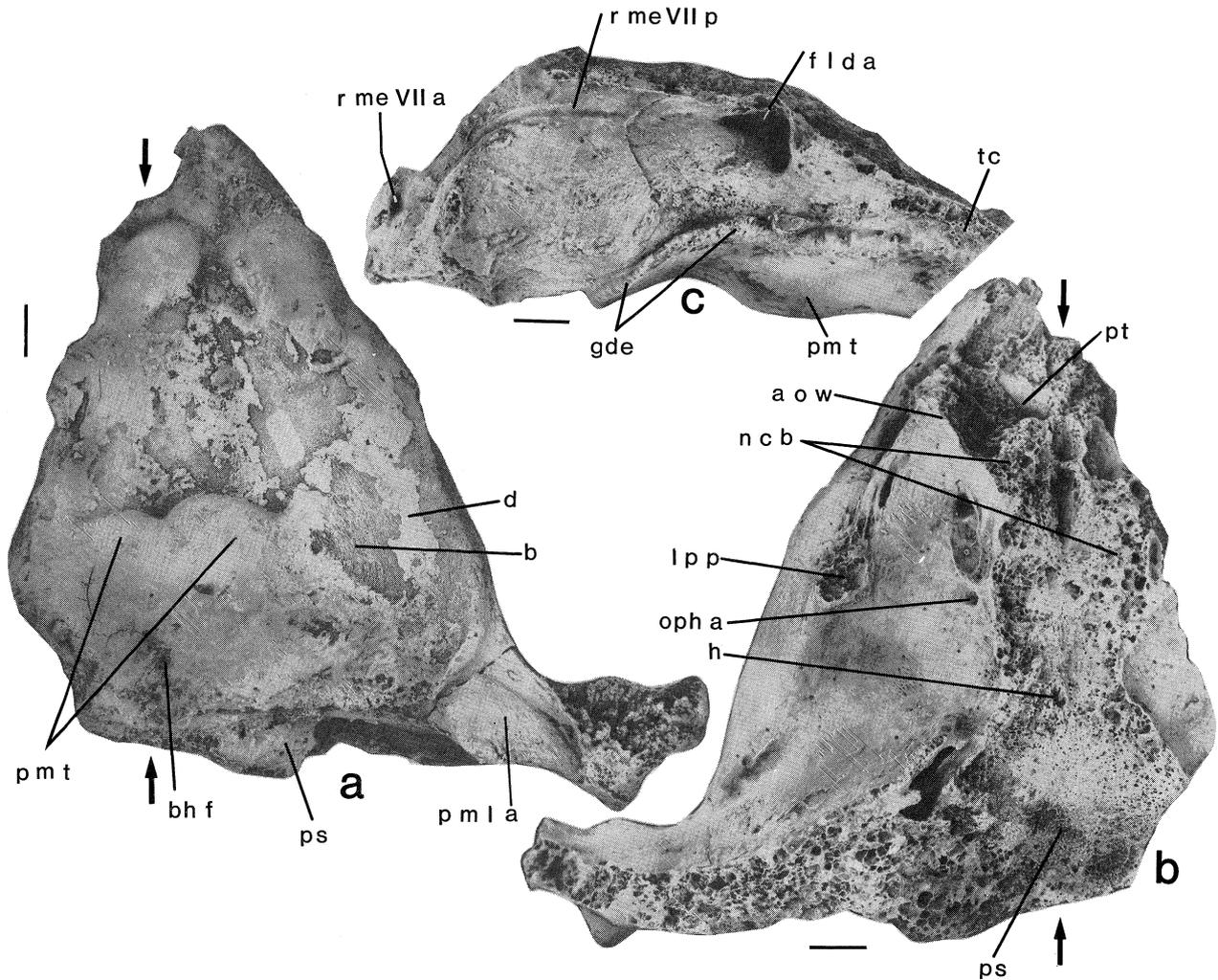
Fig. 5. The largest known palate of the species ANU36510 in ventral, dorsal and posterolateral views. In (a) note the patchy preservation of the thin superficial dentine layer which splits and peels away to expose a basal layer with vertical canals of uniform size as shown on Figure 6b. The lineations in the region marked 'b' are growth lines. This part of the palate occludes with the massive tuberosities on the mandible. a o w = antorbital wall; b = pterygoid bone showing growth lineations; bh f = buccohypophysial foramen; d = superficial dentine layer; f l d a = foramina for lateral dorsal aorta; gde = growing dentine edge; h = hypophysial stalk; l p p = lateral palatal process; n c b = neurocranial bone; p m l a = pterygoid mandibular ligament attachment; pm t = posteromedian palatal tuberosity; ps = parasphenoid; pt = pterygoid; r me VII a and p = foramina and grooves for anterior and posterior rami of the mandibularis externus VII; tc = encrusting tabulate coral *Syringopora*.

Specimen ANU35610 shows one important feature not previously recognised in a dipnorhynchid. The outer extremity of the quadrate above the jaw articulation is preserved, and it carries a canal through from the posterior face to open anterior to the jaw articulation, precisely as does the canal interpreted as carrying the r. mentalis externus VII in *Chirodipterus australis* (see Miles, 1977, figs 34, 35, 37). The groove on the posterior face of the quadrate leading to this canal is incomplete, but it clearly lay dorsal to the groove interpreted above as carrying the r. mentalis externus VII. This information makes possible a reinterpretation of the facialis branches in *D. sussmilchi* given by Campbell &

Barwick (1982a, figs 11, 12). The groove labelled 'r. hyomandibularis VII' must be one division of the mentalis externus branch of that nerve, and the one labelled 'mentalis externus VII' is a second anterior branch of the same nerve. We reach this conclusion because the latter branch clearly passes behind the articulation to enter the mandible from a posterior direction at a small foramen labelled 'f me VII p'. Only a nerve can follow such a course and judging from *Neoceratodus forsteri*, the only possible nerve is the r. mentalis externus VII. The r. mentalis internus VII follows a more ventral course.

The mandible is a massive structure (see Table 1). It
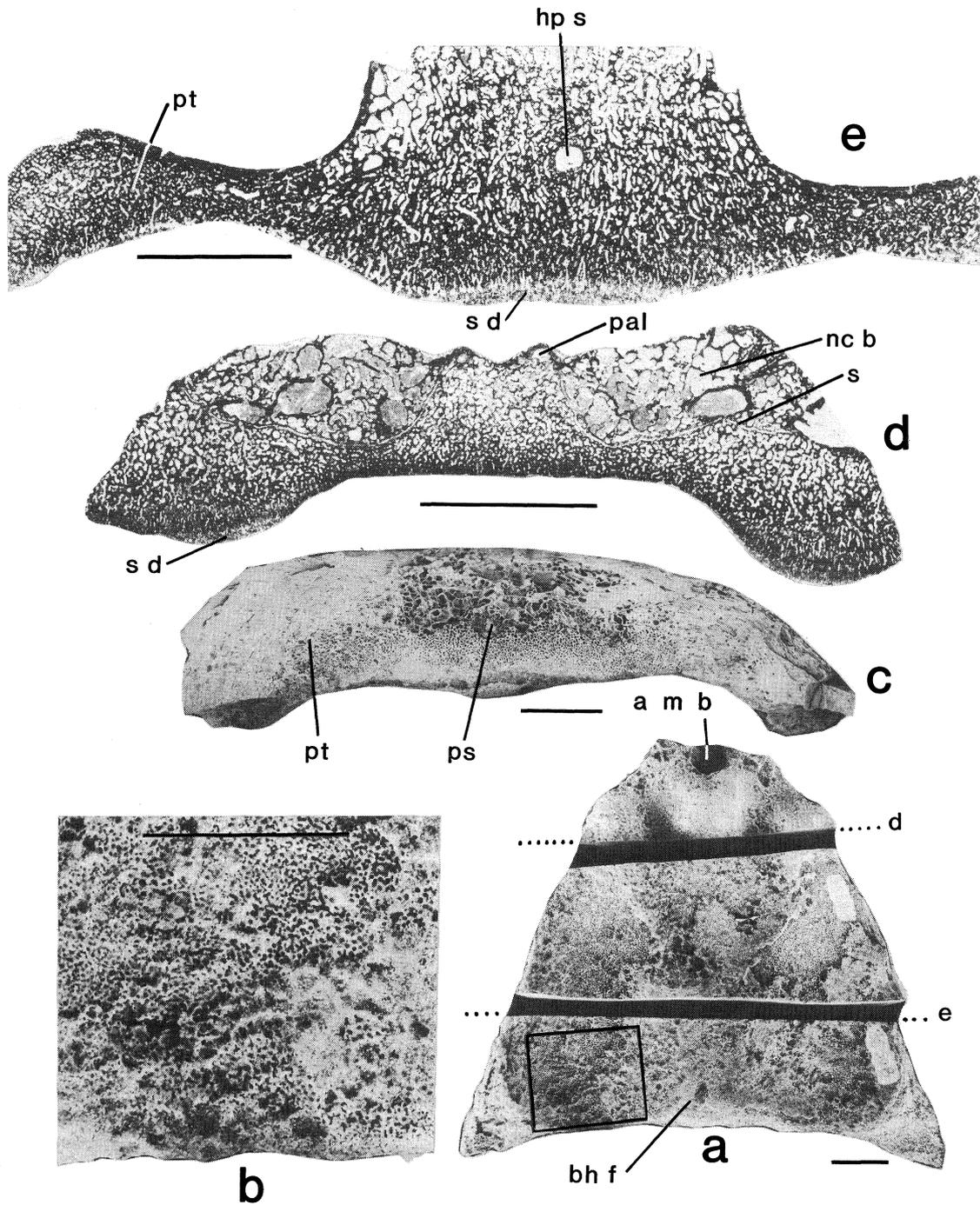
Fig. 6. a, The palate of a small specimen ANU36508 from which most of the surface layer of dentine has been removed except on the tuberosities. The two 'dermopalatines' and the anterior median bone have been lost, leaving rough bone edges; b, enlargement of the posterior part of the palate indicated on (a). Note the regular pattern of fine canals; c, posterior view of the same specimen showing the coarsely vesicular bone of the parasphenoid contrasted against the denser bone of the pterygoids and tissue of the palatal covering with its very fine canals; d, and e, thin sections taken from the positions shown on (a). In (d) note the sharp division between the canal-bearing vesicular neurocranial bone and the much denser pterygoids, the absence of a suture between the two pterygoids, and the thickening of the dentine on the tuberosities. This section was cut before the specimen was etched from the matrix and hence the cavities are filled with carbonate. Section (e) was cut after etching. In (e) note the narrow hypophysial stalk, the coarsely vesicular bone in the upper part of the parasphenoid, the continuity of the even textured bone across the palatal surface and the absence of any sutures bounding the parasphenoid. a m b = space for anterior median bone; bh f = buccohypophysial opening; hp s = hypophysial stalk; nc b = neurocranial bone; pal = palatine nerve; ps = parasphenoid; pt = pterygoid; s = suture between neurocranium and pterygoid; s d = superficial dentine layer on medial and anterolateral tuberosities.
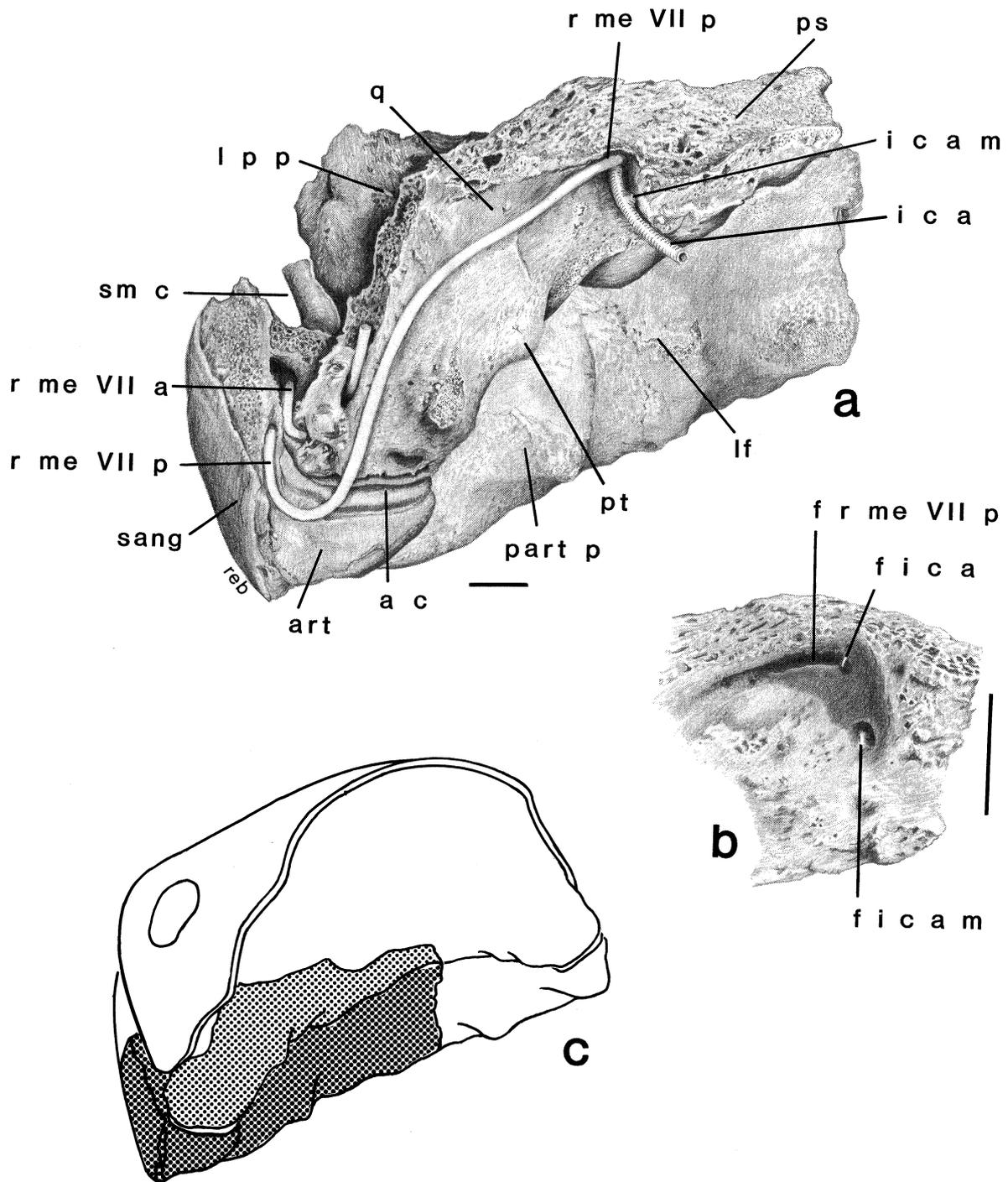
Fig. 7. Reconstruction of the left articular region of a skull and mandible in posterodorsolateral view, based on ANU35610 and AMF64832. a, reconstructed nerves, vessels and foramina; b, enlargement of the complex foramen for the facialis nerve and internal carotid artery to show the several small foramina it encloses; c, outline diagram of posterior face of skull in perspective to show location of Figure 7a. a c = articular cartilage; art = articular; f i c a = foramen for internal carotid artery; f i c a m = foramen for internal carotid artery, medial branch; f r me VII p = foramen for the ramus mentalis externus VII, posterior branch; i c a = internal carotid artery; i c a m = internal carotid artery, median branch; l f = lingual furrow; l p p = lateral palatal process; part p = prearticular process; ps = parasphenoid; pt = pterygoid; q = quadrate; r me VII a and p = ramus mentalis externus VII anterior and posterior; sang = surangular; sm c = suprameckelian cavity. Scales = 10 mm.
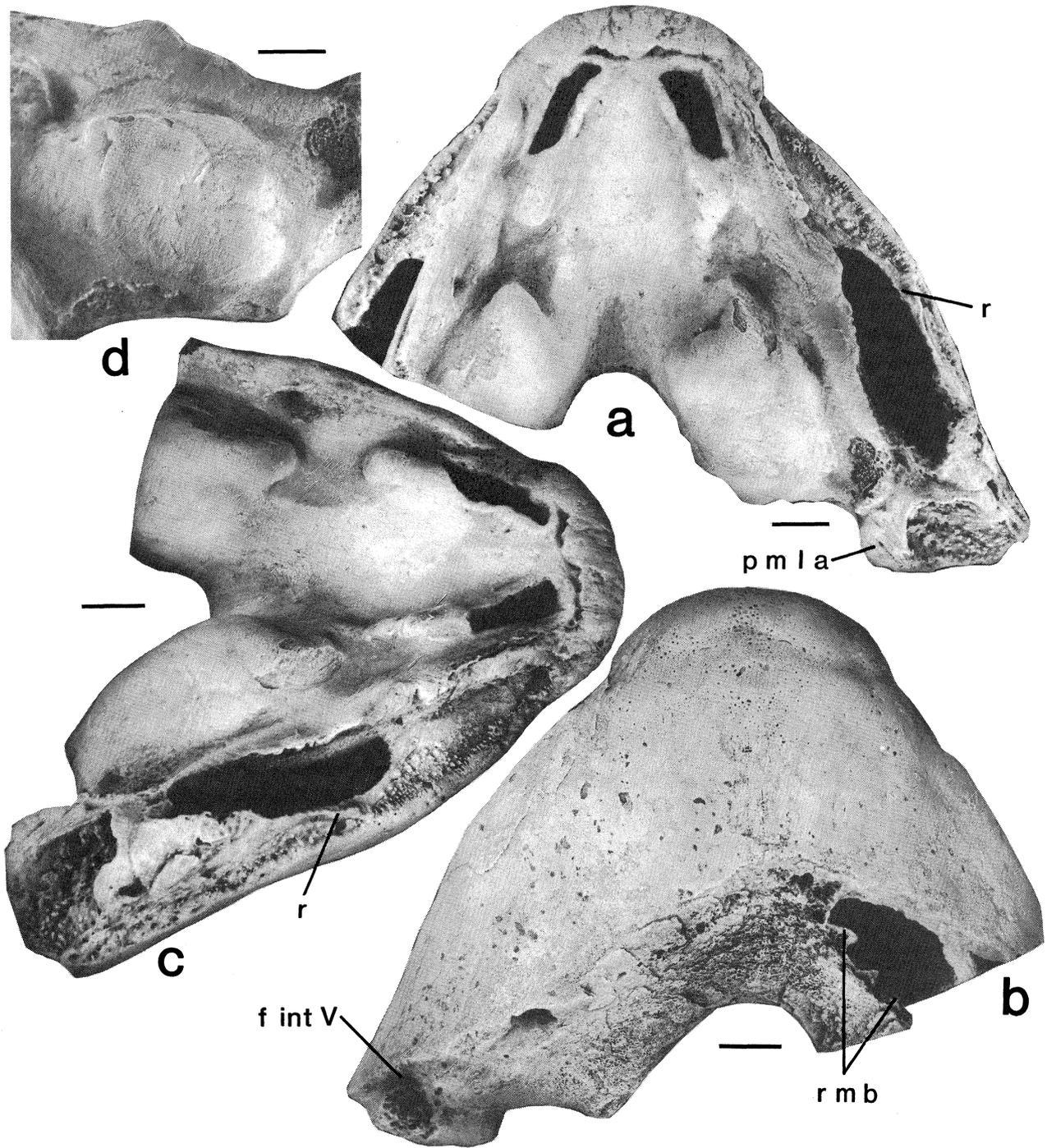
Fig. 8. a, Dorsal, b, ventral and c, oblique view of ANU35643; d, posteromedial view of the right 'prearticular' tuberosity showing the composite nature of the structure with its three surfaces at slightly different levels, the anterior one being the highest. p m l a = pterygoid mandibular ligament attachment; r = ridge separating the vertical and horizontal parts of the dorsal lamina on the 'surangular'; f int v = foramen for ramus intermandibularis V; r m b = ridges on Meckelian bone lining the prearticular face of the Meckelian cavity. Scales = 10 mm.
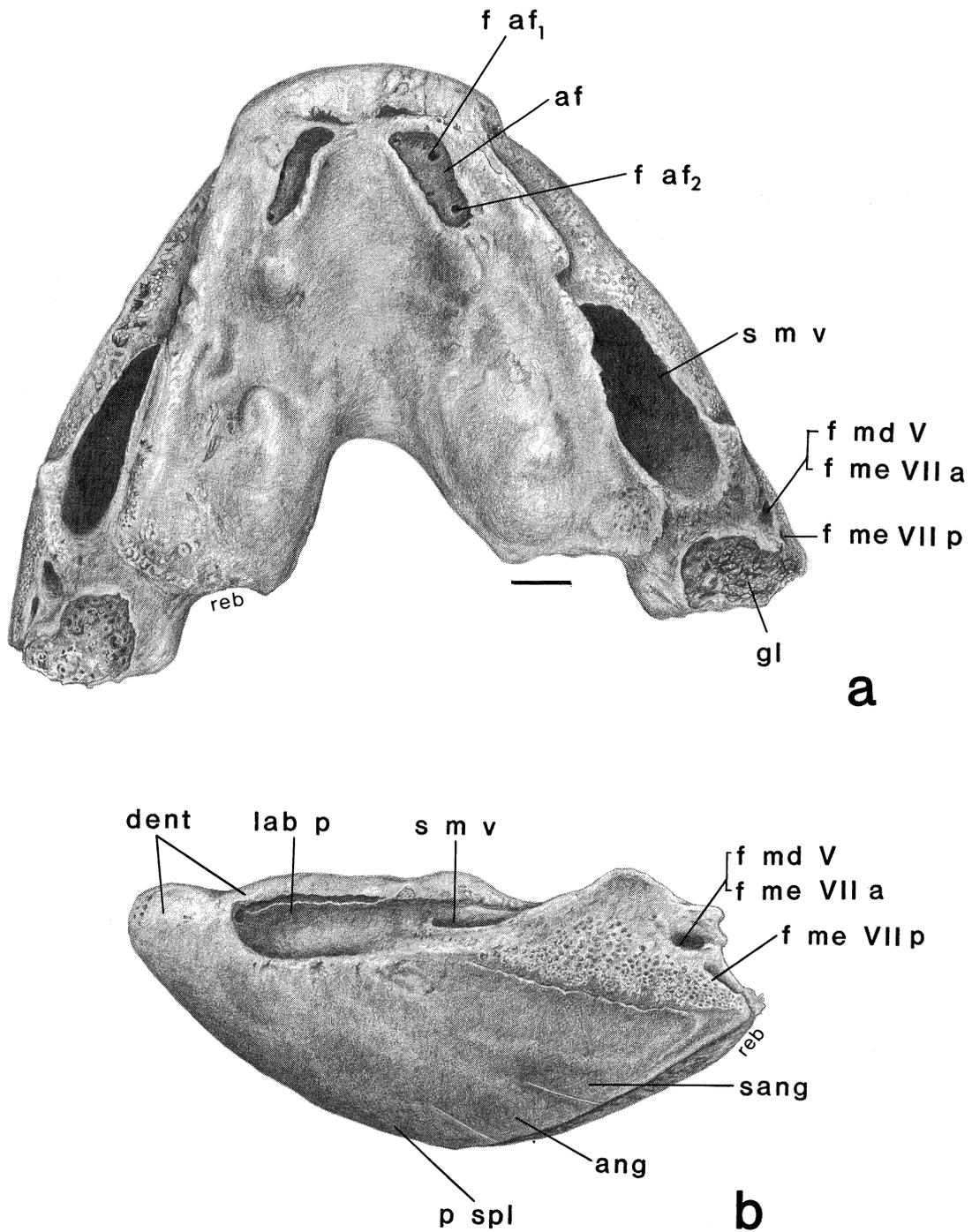
Fig. 9. Reconstruction of the mandible based on ANU35643 and AMF64832 to show details of the labial pit, the anterior furrow, the dorsal surface of the surangular and the glenoid fossae. a, dorsal view; b, left lateral view. af = anterior furrow; ang = angular; dent = dentary; f af_1 and $_2$ = foramina in anterior furrow; f md V = foramen for ramus mandibularis V; f me VII a and p = foramina for ramus mentalis externus VII, anterior and posterior; gl = glenoid fossa; lab p = labial pit; p spl = post splenial; sang = surangular; s m v = suprameckelian vacuity. Scales = 10 mm.

Table 1. Key measurements of skull roof, palates and mandibles in *Dipnorhynchus kurikae* n. sp.

Skull Roof	ANU35674	ANU35675	
Length from anterior of 'D' to posterior of 'B'	108*	82*	
Palates	**ANU36508**	**ANU36509**	**ANU36510**
Total width across articulation	—	132*	188*
Max. width of dentine bearing surfaces	74	82*	120*
Total length of pterygoids	74	—	120*
Mandibles	**ANU35643**	**AMF64832**	
Total length	92*	—	
Total width	139*	156*	
Symphysial length	66	—	

* estimated values; all dimensions in millimeters

also has been illustrated previously as *D. sussmilchi* (Campbell & Barwick, 1983, figs 4, 6). The specimen from Buchan, Victoria, illustrated by Thomson & Campbell (1971, figs 48–50) probably belongs to this species also. In most respects the mandible is close to that of *D. sussmilchi*, and hence it is not described in detail. The following are the most significant points.

Specimen AMF64832 shows the articulatory region superbly. The foramen previously interpreted as carrying 'r. mandibularis V' in dipnorhynchids certainly has a finished surface across the top of the preglenoid process for the passage of that nerve, and we confirm that interpretation. On the other hand, as shown above, one branch of the 'r. mentalis externus VII' passes in front of the articulation and must have entered this foramen also, exactly as in *Chirodipterus australis*. Other foramina and grooves and canals inside the Meckelian cavity are as in *D. sussmilchi* and *S. iani*.

The Meckelian bone forming the posterior margin of the jaw between the 'prearticular' and the external dermal bones is massive, and is well shown on AMF64832 where its boundaries are enhanced by weathering. It is exposed almost to the mid-line (Fig. 10b).

On the ventral surface the dentary is very short extending back only as far as the anterior end of the labial pits. Its posterior edge is marked by a broad shallow groove. On the dorsal surface it forms a prominent marginal tooth ridge that extends back almost to the anterior end of the suprameckelian vacuity and, as is normal in these primitive genera, it has a relatively sharp contact with the Meckelian bone that forms the floor of the labial pit. Across its dorsal surface in front of the anterior furrow the dentary has a pronounced furrow which at first sight may be thought to define the posterior edge of the bone. Its relation to the adsymphysial plate is obscure though fusion has clearly taken place. The dentary and the adsymphysial plate are approximately on the same level whereas in *D. sussmilchi* the adsymphysial plate is much lower.

The surangular is a deep bone that extends forwards to the anterior end of the labial pit. Posterodorsally it has the usual thin vertical blade covered with cosmine-coated beads. This is separated from its anterodorsal margin by a sharply defined keel in front of which the surface is abruptly inflected forming first the edge of the suprameckelian vacuity and then the floor of the labial pit. This large flat surface has cosmine-coated beads along its outer edge only. The splenial, postsplenial and angular are easily distinguished and are similar to those of *D. sussmilchi*. They are all long bones — much longer than their homologues in *Speonesydrion iani*.

The lateral line canals are deeply buried but their course can be followed by the presence of pores. One interesting feature is that the oral canal does not open posteriorly on the surangular (cf. Miles, 1977, figs 108, 109). The branch of the 'ramus mentalis externus VII' that enters the jaw through the more posterior of the two foramina lateral to the articulation, runs forwards along the inner face of the surangular, and connects with the oral lateral line canal by a row of pores.

The prearticulars have a high marginal ridge where they join the dentary, but this rapidly decreases in height along the inner edge of the suprameckelian vacuity. An elongate tuberosity lies immediately behind the anterior furrow, and a massive tuberosity forms the bulk of the tooth plate surface. These structures are high and well rounded, and the one on the right side of ANU35643, which is preserved entire, is clearly a composite structure (Fig. 8d). To maintain such shapes there must be differential growth from the base, and remodelling of both the bone and the dentine that form the mass of the tuberosity is required. The process by which this takes place requires further study, but presumably it is comparable with the process by which the cushions on the heels of the tooth plates of *Speonesydrion* are produced. This matter, and the nature of the dentine involved are discussed and figured by Campbell & Barwick (1983). Both features are discussed below.

In the floor of the anterior furrow one or two large foramina and several small ones open down into tubules within the symphysial space. A large foramen in its posterior angle leads to a posteriorly directed canal that opens into the Meckelian cavity. Another large foramen in the anterior extremity of the labial pit opens into the symphysial space. In all these features it is a typical dipnorhynchid.
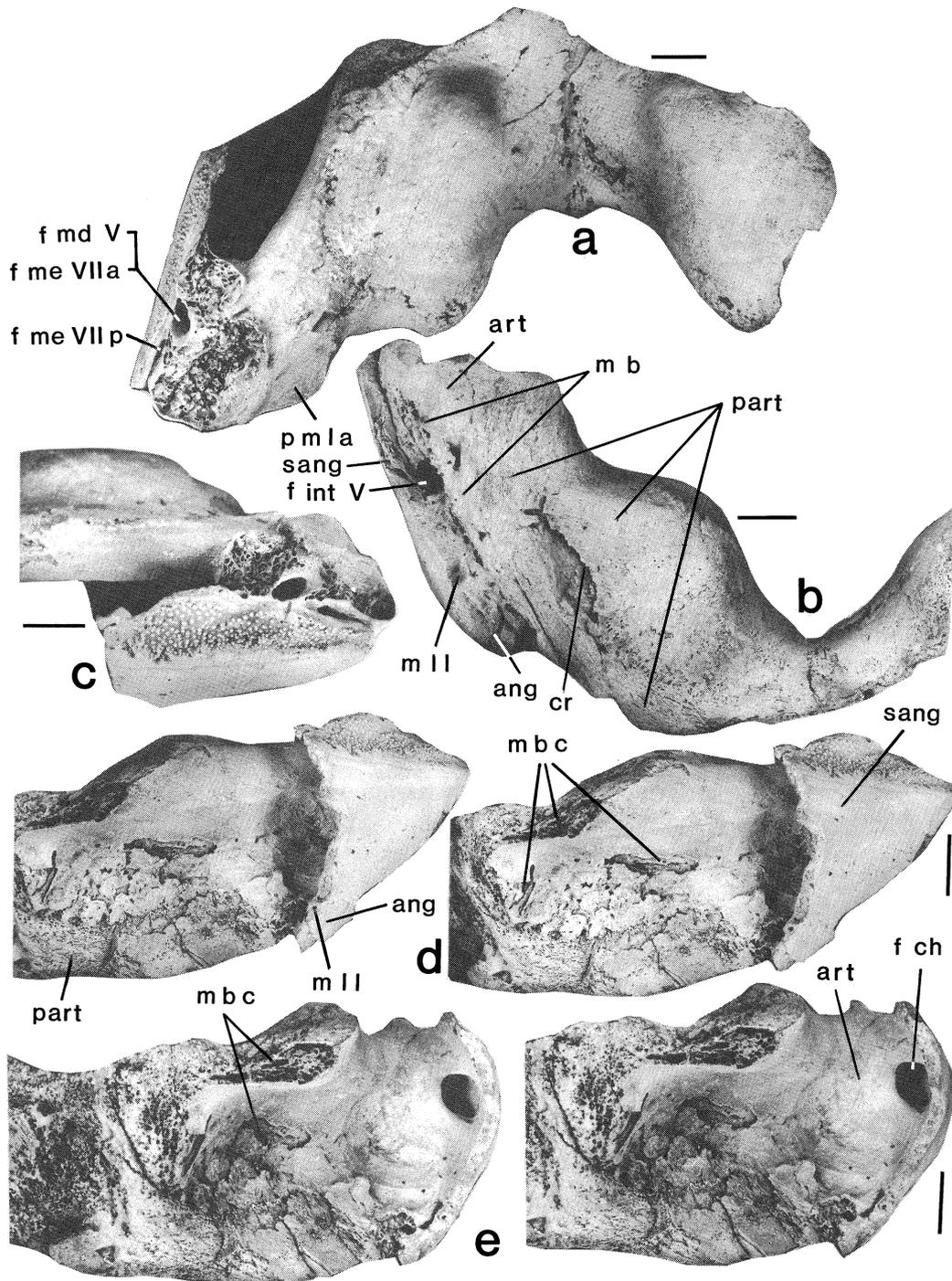
Fig. 10. Several views of the largest known mandible, AMF64832. a, dorsal and b, posterior views. Note the ragged edges of the dentine around the posterior dedges of the tuberosities in (a), and the striations on the prearticular in (b). A large crack separates the main part of the heel of the prearticular from its posterior wall. c, dorsolateral view of part of the left ramus to show the foramina and canals for the r md V and the two branches of r me VII; d, stereopair of a lateral view of the left ramus. Note the vertical blade and the Westoll lines on the 'surangular'. e, stereopair of a view from the anterior into the left Meckelian cavity. Note the thick Meckelian bone lining the floor, inner wall and roof of the cavity, and the numerous canals visible where the bone has been broken. The canals are as in *D. sussmilchi* and *S. iani* (Thomson & Campbell, 1971, figs 21, 22; Campbell & Barwick, 1984b, figs 24, 25). The foramen f ch passes out of the articular separated from the 'surangular' only by a thin sheet of Meckelian bone. ang = angular; art = articular; cr = fracture within the prearticular; f ch = foramen leading to chamber in the articular; f int V = foramen for ramus intermandibularis V; f md V and f me VII a = foramen for ramus mandibularis V and ramus mentalis externus VII, anterior branch; f me VII p = foramen for ramus mentalis externus VII, posterior branch, which runs forwards through f ch immediately inside the oral lateral line canal; m b = meckelian bone; m b c = neurovascular canals in the meckelian bone; m l l = mandibular lateral line; part = prearticular; p m l a = pterygoid-mandibular ligament attachment; sang = surangular.

Summary. *D. kurikae* was a durophagous feeder after the style of *D. sussmilchi*, but it had a much more massive head with an extremely thick palate. The space for the adductores mandibulae was enormous and its bite must have been very powerful. The associated rich marine invertebrate fauna leaves little doubt that like *D. sussmilchi* it fed on hard shelled invertebrates.

It occurs in slightly younger strata than *D. sussmilchi*, and in the same area. Hence it could be expected to be a more advanced species. This is consistent with the fact that in all the characters in which the two species differ, *D. kurikae* is considered to be the more derived form. This applies not only to the remarkable specialisation of the palate and mandible for feeding but also to the reduction in 'D' bones, the increase in the size of 'X' and the division of the anterior furrow by the forward movement of the adsymphysial plate.

Speonesydrion iani occurs in the same bed at the same locality. Its 'D' bones and the anterior roofing bone pattern are more primitive, but the position of 'K' and the interrelations of the lateral lines in the 'X'–'K' area are more advanced than those of *D. kurikae*, if we accept the polarities of these characters outlined by Westoll (1949) and Miles (1977). There is no possibility of confusing these two genera in the collections. *D. kurikae* has more massive external dermal bones, a narrow snout, crudely differentiated dental apparatus and a less massive mandible, in addition to the characters listed above.

PHYLOGENETIC POSITION OF THE DIPNORHYNCHIDS

Species of *Speonesydrion* and *Dipnorhynchus* have been regarded as close relatives. Indeed *S. lehmanni* was first described as a species of *Dipnorhynchus* and was still considered as such by Miles (1977). The two genera, represented by two and three species respectively, share a number of distinctive characters — thick dentine-covered palates that increase their area by the incorporation of denticles around their free margins, dentine covering the floor of the lingual furrow and heavy tuberose heels on the prearticulars.

With the most primitive denticulate genus *Uranolophus* (see Campbell & Barwick, 1983) dipnorhynchids share the complex plating of the anterior skull roof, the meeting of the 'I' bones behind 'B', the separation of the lateral line canal in 'J'–'K'–'L' from that in 'Y$_2$'–'X', the fusion of the parasphenoid with the pterygoids and the large mandibular anterior furrow which is enclosed at its posterolateral extremities. Members of the denticulate group, however, have a number of distinctive features from the time of their appearance — the nature of the shedding denticles, thin palates, marginal ridges and the absence of buccohypophysial and pineal openings. Details are given by Campbell & Barwick (in press). There is no doubt that the two groups had a common ancestor which preceded them by a short interval. But it is equally clear that they had established different feeding modes that were to form the basis of two distinct lineages.

The most interesting evolutionary feature to be explored now is the relationship between the dipnorhynchids and other non-denticulate dipnoans. Given that they are the most primitive members of the 'plated' or 'dentine retaining' lineage, how are the component species related to one another and to later Devonian genera such as *Dipterus*, *Scaumenacia* and *Chirodipterus*? Of course the first of these questions points up the crux of the matter. Are the dipnorhynchids really a homogeneous group as has been commonly assumed? *Dipnorhynchus* has been regarded as the more primitive genus because its members have such crudely moulded dentitions (White, 1965; Thomson, 1967), more massive mandibles and less advanced roofing bones around 'K'. However, the matter is not as simple as that. *S. lehmanni*, from the Siegenian, is the oldest member of the group; this is suggestive but not conclusive evidence of its more primitive status. Moreover the concept of crudity of dentition as applied to these genera has no validity — the two types of dentition result from distinct developmental strategies. This type of evidence is of much greater value than roofing bone patterns since the latter are very labile even within a species, and are known to show considerable convergent and parallel evolution. Consequently the dental structures need further comparative study.

The palatal dental surfaces of species of both genera grow around their free margins only. Dentine completely covers the parasphenoid/pterygoid and pterygoid/pterygoid sutures, and consequently no bone growth can take place along these sutures without massive dentine resorption. There is no evidence that this has occurred. Additions to the lateral and posterior margins of the *Dipnorhynchus* palate took place by the growth of denticles of various sizes and their gradual incorporation into the dentine-covered surfaces by continued growth, wear and some resorption. This type of addition is well seen on the posterior and lateral parts of the palates of both *D. sussmilchi* and *D. kurikae*. The prearticular dental surfaces expanded by a similar process, and the denticles in the lingual furrow are remarkably well developed and illustrate the mechanism with great clarity.

As has been indicated above, the growth of the massive tuberosities of *Dipnorhynchus* cannot take place by the addition of large bodies of dentine at the plate margins. In the first place the dentine on them is not unusually thick, and in the second place they must migrate across the palate with growth or they would not be in a similar position on all specimens regardless of size. The only way this can be accomplished is for differential wear to occur in some areas, those that are protected by the hardest and thickest dentine gradually rising above the surrounding areas (Fig. 11). The dentine would maintain itself by pleromic growth into the underlying bone, the rate of its development in different areas being such that the tuberosities could migrate across the palate. In other words, the outline of the
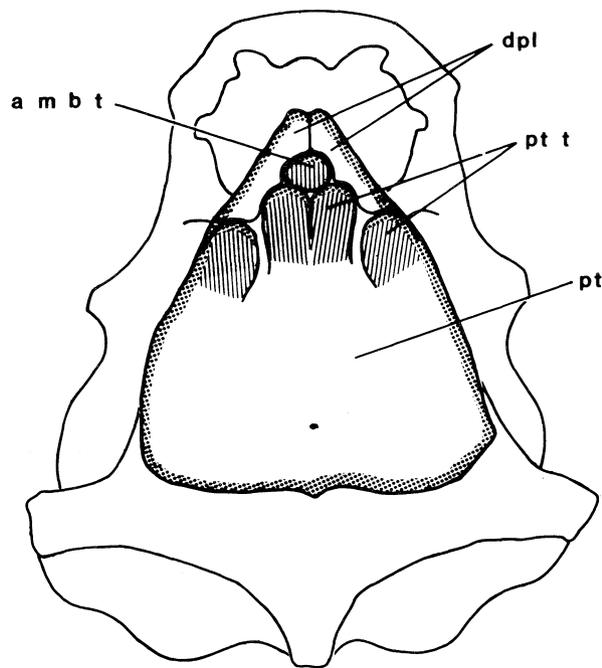
Fig. 11. Reconstruction of the palate of *D. sussmilchi*, in ventral view showing the zones of areal increase of dentine (stippled) and the zones of wear on the tuberosities (hatched). Note that as a result of this pattern, the tuberosities on the pterygoid and the anterior median bone migrate forwards and outwards, dentine growth takes place at the anterior margins of the tuberosities and the anterior and lateral margins of the pterygoids and the 'dermopalatines'. a m b t = anterior median bone tuberosity; dpl = 'dermopalatines'; pt t = pterygoid tuberosities.

palatal plates would be determined by the varying rates of marginal addition, whereas the relief on their surfaces would be determined by differential dentine growth and differential wear within the bounds of the established plate margins.

Species of *Speonesydrion* adopted a different mode of growth. Their lateral palatal margins increased by the addition of teeth which are aligned to form rows. These teeth range from simple cones to groups of denticles on the flanks of what is, in effect, an enlarged denticle (Campbell & Barwick, 1984b). Between the teeth, denticles of various shapes grew and became worn, finally coalescing at their bases to form a continuous dentine sheet crossed by radial ridges that were formed from the worn bases of old teeth. Posteriorly the plates must have expanded by the gradual incorporation of denticles in the same way as *Dipnorhynchus* plates, although the details are not so well known in the absence of good material. The prearticular plates developed radial ridges in the same way as palatal plates. The means by which they expanded is particularly well known (Campbell & Barwick, 1983, 1984b). The heel of the prearticular plate developed tuberosities by differential pleromic growth in the same way as the heel and palate of *Dipnorhynchus*.

In summary then, the plates of the two genera are similar in that they increase marginally by the incorporation of denticles, they have no bounding layer of enamel as does *Sagenodus* or *Ctenodus* and all subsequent genera, and they both produce tuberosities by similar processes. They differ in that *Speonesydrion* has differentiated the denticles on the lateral margins to produce prominent teeth which are added according to a distinctive pattern to produce plates with a small number of teeth in a small number of rows. Such plates clearly are tooth plates of the classic dipnoan type, but they are rudimentary. *Dipnorhynchus* on the other hand produces crudely sculptured plates only by differential internal growth and wear without the special modification of marginal denticles to form teeth.

Differences at this level are apparently slight, but they had profound consequences. The next member of the tooth plated line is *Dipterus*. It retained many primitive features such as a complete cosmine cover on the external dermal bones, a large number of bones on the anterior part of the skull roof and a buccohypophysial opening, but it had lost the pineal opening, separated the dentine cover on the pterygoids thus permitting growth in the mid-line, lost the dentine on the parasphenoid which in its turn had become elongated, reduced the strength of the lower jaw and produced more delicate sculpture on the tooth plates. Later members of the lineage, such as *Scaumenacia*, lost their cosmine, reduced or lost the snout ossification, decreased the number of anterior roofing bones, developed more regular radial tooth rows and laid down a continuous layer of enamel around all margins of the tooth plates. Accompanying these changes there were considerable modifications to the histology of the tooth plates. These have been outlined by Smith, Smithson & Campbell (in prep.).

The genera that developed tuberosities rather than teeth, and thus produced dentine plates rather than tooth plates in the terminology of Smith & Campbell (in prep.), followed somewhat different evolutionary lines. The next members of this lineage after *Dipnorhynchus* are *Stomiahykus*, from the Eifelian and *Chirodipterus* from the Frasnian. In these genera the marginal denticles were modified into elongate blisters which added bodies of dentine to the margins of the plates, and they began to develop radially arranged tuberosities composed of hard pleromic dentine. It is interesting that *Stomiahykus* retains 'dermopalatines' fused to the pterygoids, pterygoid plates meeting in the mid-line, a parasphenoid fused to the pterygoids, and dentine on the parasphenoids, whereas *Chirodipterus* has free 'dermopalatines' that do not meet medially, separated pterygoids and parasphenoid, and no dentine on the parasphenoid. In addition the plates of *Chirodipterus* have developed petrodentine (Smith, 1984). Like the roofing bone changes referred to above, these changes parallel those of the tooth-plated genera.

If *Speonesydrion* is the first known member of a lineage leading to tooth-plated types and *Dipnorhynchus* is in a comparable position in relation to dentine-plated types, the Dipnorhynchidae would be a grade group or, in cladistic terms, a paraphyletic group.

If Smith and Campbell are correct in separating tooth-plated and dentine-plated types into distinct lineages, and it seems impossible to convert one type into the other, the amount of parallelism within these lineages like that between the denticulated lineage and the plated lineages together, is very considerable. Once again attempts to infer relationships by seeking to minimise parallelisms and convergences on the grounds that such a procedure satisfies the requirements of parsimonious argument, is called into question. The nature of the genetic code should have alerted us to the point that parallelism and convergence could be expected to be a widespread rather than an exceptional result of the evolutionary process. This is now being exemplified by such work as that of Sibley and Ahlquist (1985) on Australian passerine birds. What is needed for the elaboration of the palaeontological data is more sophisticated analysis of comparative morphology and less speculation based on philosophical presuppositions about the nature of the evolutionary process.

THE PRIMITIVE DIPNOAN PLATE

The morphotype from which tooth plates and dentine plates were derived can now be reconstructed. We hypothesise that it had the following characteristics: (a) continuous dentine across the pterygoids and the lingual furrow, precluding the addition of dentine in the mid-line in either jaw; (b) addition of dentine at the lateral and posterior margins of the pterygoids and prearticulars by the incorporation of denticles of uniform size; (c) lack of differential pleromic growth on the plates except perhaps for the heel of the prearticulars; (d) absence of radial ridges or any other eminences on the plate surfaces, as the result of the above growth patterns; and (e) thin dentine with irregular pulp canals growing directly on the basal bone and with a minimum of bone resorption to permit downward dentine growth.

Note that this hypothesis requires the presence of denticles around the plate margins. These denticles were attached to the basal bone and were gradually incorporated into the continuous dentine sheet. They were not of the shedding type which characterised the denticulate lineage of Campbell & Barwick (1983). Dealing with a similar case of confusion resulting from a failure to recognise comparable entities of different origins Read (1948) noted that there are 'granites and granites'. We reiterate that in our view there are 'denticles and denticles'.

So far as can be determined at present, the Dipnoi differentiated from other bony fishes by the development of a palatal bite. Associated changes were the holostylic jaw suspension, the development of distinctive muscle chambers in the cranium and unique cristae to brace the roof to the braincase, the evolution of the broad mandible with larger open rami for the insertion of the adductor muscles and the covering of the palate and the 'prearticulars' with hard-wearing dentine. As we have shown elsewhere, it is not possible to homologise the bones of the palate with those of tetrapods (Campbell & Barwick, 1984a), and it has long been known that there are major difficulties in accounting for the absence of such bones as the coronoids in the mandible. Despite attempts to show that premaxillae and maxillae are present as modified tooth bearing bones in early dipnoans, supporting arguments have been shown to be dubious (Campbell & Barwick, 1984b). Skull roof differences are also manifest. The Dipnoi is the only group which primitively has five longitudinal rows of bones across the posterior part of the roof (Schultze & Campbell, in press), and the arrangement of the lateral line canals on the skull and mandible is distinctive (Gardiner, 1984).

The time has come to consider seriously the argument, based on the excellent fossil material now available, that this type of organism with its palatal bite became separated from other bony fishes before the premaxillae, maxillae, distinctive roofing bone patterns, pterygoids, 'dermopalatines', dentaries, prearticulars and coronoids differentiated from the matrix of small dermal bones in ancestral osteichthyans. Such an analysis is now feasible and could be undertaken to counter the views on the phylogenetic relationships of the Dipnoi derived from comparison of the highly derived characters of the extant genera of the group (Rosen et al., 1981).

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