The Braincase, Mandible and Dental Structures of the Early Devonian Lungfish *Dipnorhynchus kurikae* from Wee Jasper, New South Wales

K.S.W. CAMPBELL AND R.E. BARWICK

Geology Department, Australian National University, Canberra A.C.T. 0200, Australia

ken.campbell@anu.edu.au

richard.barwick@anu.edu.au

ABSTRACT. *Dipnorhynchus kurikae* Campbell & Barwick was described from the *Receptaculites* Limestone Member at Wee Jasper. Our new specimens include material of the braincase, the snout, the nasal capsules, the palate and the mandible which were not previously available. The new specimens give new data on the pores in the snout, the arrangement of the soft tissues in the nasal capsule, the growth of the hard tissues on the surface of the dentary, the formation of the hard surface on the palate and the prearticulars, the arrangement of sacculus and the nerves VII, IX and X in the otic region, and the interpretation of the palatoquadrate. The lateral lines on the mandible have been exposed by excavation. Thin sections show that the bone on the overgrowth of the dentary is of the same kind as occurs in the cores of the ridges on the tuberosities and marginal ridges on the palate and prearticular. A thin layer of dentine-like columns which contain no dentine tubules overlie the bony cores. This, and the mode of growth, demonstrate that the dental plates—being made of a bony core—have different patterns of deposition from tooth plates in most later Palaeozoic genera, which are made of dentine. This throws light on the way tooth plates evolved from a dipnorhynchid pattern through a speonesydrionid pattern to true tooth plates. The complex tooth plates of *Diabolepis* are considered to be independently developed. Ventrally the parasphenoid of *Dipnorhynchus kurikae* does not divide the pterygoids, but stops short at the posterior end of the pterygoids. The semicircular canals and the superior sinus of the saccular cavity are described from the well-preserved material. In comparison with *D. sussmilchi*, this species has a number of distinctive features, and is easily recognised as a separate species.

CAMPBELL, K.S.W., & R.E. BARWICK, 2000. The braincase, mandible and dental structures of the Early Devonian lungfish *Dipnorhynchus kurikae* from Wee Jasper, New South Wales. *Records of the Australian Museum* 52(1): 103–128.

Dipnorhynchus kurikae Campbell & Barwick, 1985, was described from two partial skull roofs, three isolated palates, two snout fragments, and two isolated mandibles. The neurocranium, the rostrum and the nasal capsules were unknown, and though the palate and lateral wings and the lower part of the neurocranium were well enough preserved, their relationships with other parts of the skull were unclear. Three new specimens of the mandible have been recovered from the type locality, including the smallest and the largest known individuals. Two new crania, one of which comes

from the type locality and the other from the same horizon about 5 km farther north, add considerably to our knowledge of the species and, though they lack roofs, they enable us to demonstrate more clearly than we could when it was first described that the species is distinct from *D. sussmilchi* (Etheridge, 1906). The oldest *Dipnorhynchus* specimens have been found in the basal part of the Cavan Bluff Limestone below the appearance of *Polygnathus dehiscens*. This suggests that they are possibly Pragian in age, making the genus the oldest or the second oldest member of the Dipnoi known at present. Morphological details of *D. kurikae* are of maximum importance because its preservation provides the best information available on the external and endocranial structures of primitive dipnoans. The new material has a section along the braincase which allows us to map out the neural features directly. One nasal capsule is fully exposed, and provides detail of the subdivision of the nasal capsule, as well as the nerves entering it.

The structure of the cheek is not known by direct observation, but reconstructions by Thomson & Campbell (1971) and (Westoll, 1989), have drawn different conclusions. Westoll concluded that all these Australian *Dipnorhynchus* are very closely comparable. Of course, this is obvious because they are congeneric; alternatively he may have been implying that a single variable species has been unnecessarily split. The present specimens add data to indicate that such a view is untenable. Westoll also interpreted the cheek of *Dipnorhynchus* with a skull that is flattened in comparison with that of *Dipnorhynchus*, and with a mandibular canal exiting from bone 4 rather than bone 5 as is normal for Devonian dipnoans.

The second partial cranium is not so well preserved, but it exposes the posterior part of the neurocranium, and a large part of the otic region. This has been known only from the holotype of *Dipnorhynchus sussmilchi*, the posterior part of which is poorly preserved, and the structures now observed permit a better reconstruction than we have had previously.

The mandibles show details of structure and the dental plates are well enough preserved to section and to examine under light microscopy and by Scanning Electron Microscopy. These sections have been compared with sections of secondary growth on the mandibles, and they are found to be closely comparable. This is of major significance for studies of the primitive dental plates in dipnoans. Similar structures are found in the tuberosities on the palate. We conclude that the animal had dental plates which had a thin layer of dentine, and were able to grow periodically by addition to bone by internal growth. The lateral lines can be excavated and show in detail their pattern. All of these features give more information on the most primitive dipnoans.

Material. The material used for this paper is as follows. SKULLS: ANU 48676, from the type locality, the base of the *Receptaculites* Limestone along a strike line of ca. 1 km around L624, of Pedder *et al*. (1970). ANU 48678 from a similar horizon, ca. 5 km north of the type locality. Rocks in this area were exposed near Cave Island during a drought. MANDIBLES: ANU 60028–60030, also from the type locality. ANU 60030 is on loan from Ian and Helen Cathles of Cookmundoon Station, Wee Jasper.

Description

The palate

Incomplete palates from four specimens are known. The most complete is ANU 48676, from which the braincase is described below (Fig. 1).

The dermopalatines are not clearly defined, but they are long and extend back to the level of the preorbital wall (Figs. 1A, 6B). Their outer edge is ridged, the posterior end having three or four rounded eminences on the ridge.

The pterygoids (Figs. 1A, 2A) are well preserved and have clear raised structures on their surfaces in some specimens, but flatter structures on others. The level of expression of these features is not related to the size of the specimens, implying a periodic reconstruction of the surfaces. The lateral margins of the pterygoids are formed of rounded ridges which, although continuous, show three or four slightly rounded eminences along their length. The most anterior ones are the most prominent, and lie against the dermopalatines—they consist of swellings which extend into the more median parts of the palate. The remainder of the lateral margin of the pterygoids extends back to the posterior end of the dental-plate, becoming narrower posteriorly. The lateral facing edges of the pterygoids have irregular denticles where lateral growth took place. In a well formed specimen, ANU 48676, the marginal ridge has a furrow against the large bosses (posterior tuberosities or blisters) that form the posterior part of the palate. White (1966: 7) referred to these elevated surfaces as raised blisters. In this paper we will refer to the elevations on the pterygoids and the prearticulars as tuberosities. On full closure these marginal ridges fit medially to the marginal ridges on the mandible. The anterior lateral tuberosities fit into the cavities behind the anterior tuberosity on the mandible.

The posterior tuberosities are variable in size and outline, but ANU 48676 (Fig. 1A) has them beautifully preserved. The anterior edge of each tuberosity has a median projection with two lobes on each side. The median projection extends forward of the others, and has a definite embayment on each side. The posterior edge of the tuberosity is broken up into irregular patches or denticles indicating that the growth took place by extension in that direction and by overgrowing these irregularities. In front of the posterior tuberosity is a large cavity in the palatal surface. *Dipnorhynchus sussmilchi* has a smaller depression which is not so well defined (Thomson & Campbell, 1971: fig. 75). The anterior median tuberosity forms a pair towards the end of the pterygoids. These tuberosities are not equal in size on the one specimen, and they fit unevenly into the median space in the mandible.

Anterior to the pterygoids but between the dermopalatines, is an open space lying anterior to the paired anterior tuberosities (Figs. 1A, 2A). In ANU 48676, the margins of the open space are rough as though a bone has fallen out. Thomson & Campbell (1971) referred to this space as being occupied by a small bone in some specimens. Such a bone is present in the specimen of *D. sussmilchi* labelled ANU 18815, but in other individuals it must have been a bone so loosely articulated with the surrounding bones that it has fallen out. With further evolution in which reduction of the dermopalatines occurs, this bone becomes isolated at the
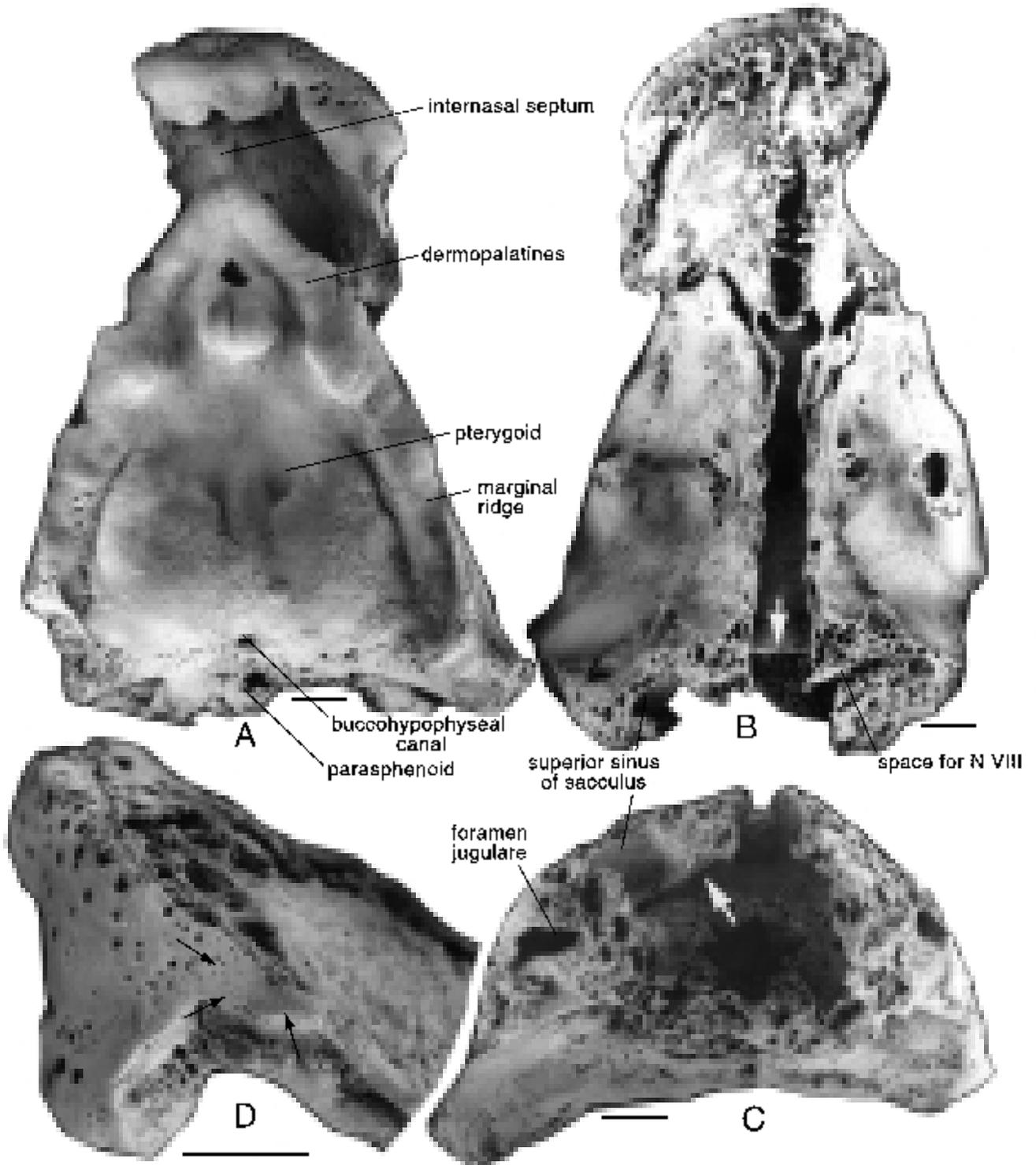
Figure 1. *Dipnorhynchus kurikae*, all parts of this figure are of ANU 48676. A,B—ventral and dorsal views of a skull from which the roof was removed during preservation. In A, note the shape of the posterior and anterior palatal tuberosities, the position of the buccohypophyseal opening, and the shape of the anterior naris. In B, note the shape of the braincase, the closely spaced neurocranial walls, the swelling on the superior sinus of the sacculus, the space for nerve VIII and the back of the endocranial wall of the braincase where it joins the notochordal cavity (white arrow). C—posterior view of the specimen. Note the end of the notochordal cavity, the position of the nerve VII on the left (white arrow), the superior sinus of the sacculus, the walls of the sacculus, and the foramen jugulare. D—view of the labial pouch and snout showing a small area of cosmine on the dermal roof. Note the large excavation for the labial pit. Scales = 10 mm.
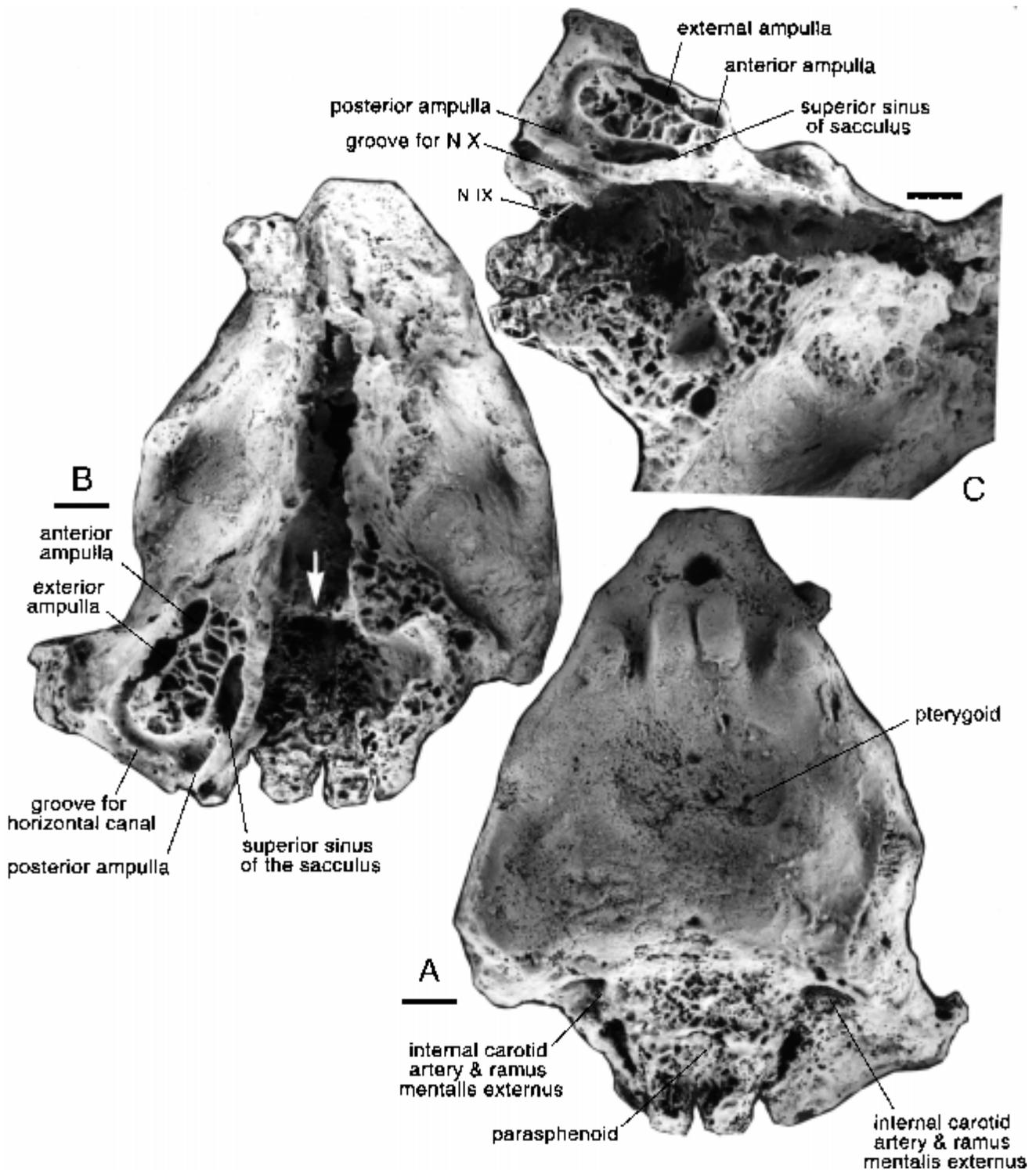
Figure 2. *Dipnorhynchus kurikae*, an isolated palate and braincase, ANU 48678. A—ventral view. Note the shapes of the tuberosities on the palate, the gross form of the parasphenoid and the position of spiracular recess. B—dorsal view, left side worn through to the level of the horizontal semicircular canal and the position of the superior sinus of the sacculus. The three ampullae of the semicircular canals well shown. Anterior edge of the notochordal cavity marked with a white arrow. See also Fig. 4A. C—dorsolateral view of the braincase. Nerves IX and X and the ampullae marked. For detail see Fig. 5. Scales = 10 mm.

front of the pterygoids (Miles, 1977: fig. 67). Although Miles (1977) refers to the isolated bone in front of the pterygoids of *Chirodipterus australis* as the vomer, we consider that the bone is not homologous with the vomers in any other group, but is a neomorphic feature in dipnoans. This is a highly significant point, as some workers consider the presence of vomers to be of significance in discussing relationships of dipnoans. For example, some workers consider that *Diabolepis* is the sister group of the Dipnoi, and it has an anterior pair of bones which are named the vomers. We see no evidence that these paired bones in *Diabolepis* (Chang, 1995: fig. 11) are the homologues of the isolated bone in dipnoans.

As was shown by Campbell & Barwick (1985: fig. 6d) cross sections of the palate show no signs of a boundary between a parasphenoid and the pterygoids on the buccal surface, but its outline is seen anterior to the buccohypophyseal tube on the dorsal surface. It was attached to the posterior end of the pterygoids, and the only way it could have increased in size was by the addition to its posterior and lateral edges. On ANU 48676 only the anterior end of the parasphenoid is preserved, but on ANU 48678 (Figs. 2A,B) most of it is present, even though the ventral surface is eroded. It rises dorsally in a sharp even curve from the palate and then turns posteriorly to make a short process. This is very similar to that of *D. sussmilchi*, which also has a median furrow that breaks through the bone in the same way. It seems to us that a thin layer of bone was present in this region, but it is not preserved. Once again, there is no similarity between the structure of the parasphenoid in these primitive dipnoans and the parasphenoids in *Diabolepis* (Chang, 1995: figs. 4, 11) which is close to that of the porolepiforms.

On the posterior wall a large recess, named the spiracular recess by Thomson & Campbell (1971), is also present in this species. This foramen was for the internal carotid artery and the ramus mentalis N VII. No matter how we interpret this opening, there is no structure like it in *Diabolepis* (Chang, 1995).

The buccohypophyseal foramen lies towards the posterior end of the palate, but its relation to the posterior end of the palatal thickening varies from specimen to specimen. It is at the end of a tube which has been described by Campbell & Barwick (1985).

The structure of the neurocranial walls

The inner perichondrium is made of continuous bone and is separated from the outer perichondrium by only 1–2 mm of endochondral bone (Fig. 1B, 3, 4). Specimens of *Holodipterus gogoensis* (Pridmore *et al*., 1994: fig. 1) and of *Chirodipterus australis* of similar size have a greater separation between the inner and outer perichondral walls than in *D. kurikae*, and the space between them is not filled with so much vesicular tissue (Fig. 1B). The foramina for the nerves and vessels are well exposed on ANU 48676, and the canals in the bone have been removed by etching with acetic acid. It has been possible for the first time to trace the canals by inserting fine nylon line into them and observing their points of emission. An examination of this kind provides the basis for Figs. 3 and 4. The structure of the braincase wall will be discussed below, beginning at the anterior end. The description will be based on the two ANU specimens which will be referred to as required.
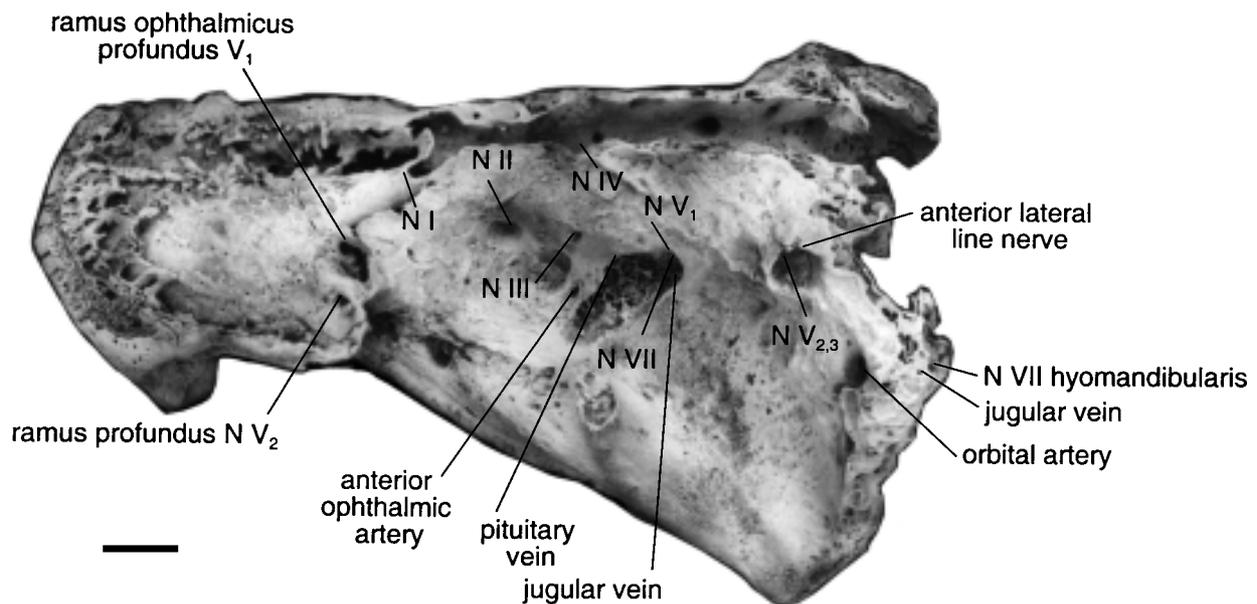

Figure 3. *Dipnorhynchus kurikae*, dorsolateral view of ANU 48676 showing the lateral features of the braincase nd the otic region. Main structures indicated and details shown on Fig. 4. Scale = 10 mm.
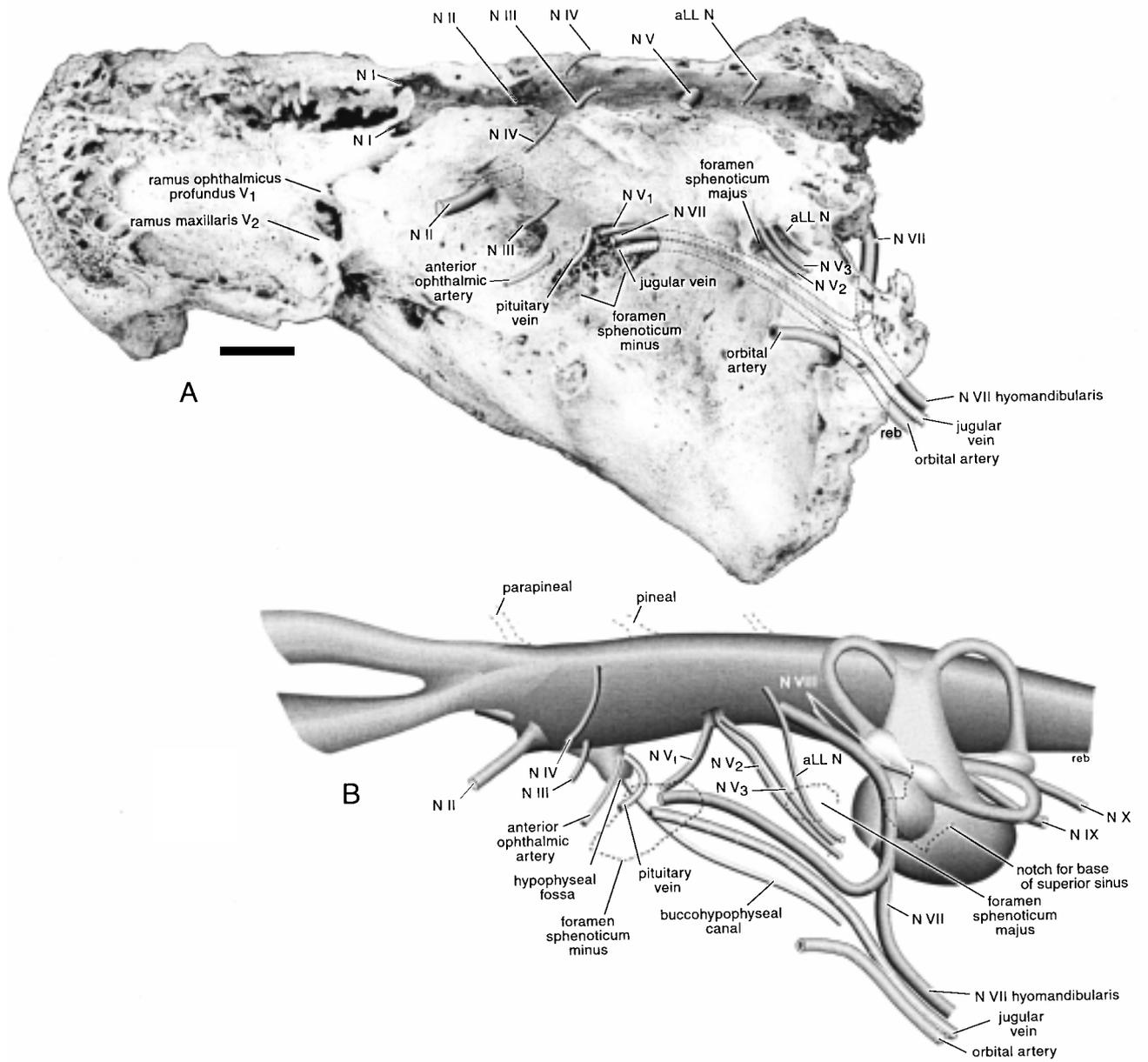
Figure 4. *Dipnorhynchus kurikae*. A—dorsolateral view of the specimen shown in Fig. 3. Nerves and vessels are indicated, with their courses shown as dotted lines where they are hidden in bone. B—reconstruction of the braincase with the dorsal surface of the braincase restored from other specimens of *D. sussmilchi*. Nerves and vessels drawn around the outline structures shown in Fig. 4A, and the otic region as in Fig. 5. The outlines of the foramen sphenoticum minus and majus, and the notch for the base of the superior sinus in Fig. 4A, shown in dotted outline. Scale = 10 mm.

Olfactory canals. The two olfactory canals separate at a point half way between the anterior end of the notochordal chamber and the tip of the snout. Each runs for 1.5–2.0 cm before opening into the nasal capsules at a junction that is marked by a slight but continuous bony rim. The walls of the olfactory canals are perforated with a number of tubules which are most common on the ventral and mesial sides, the latter joining the two sides together. Northcutt (1987: 289) commented that in *Latimeria* and *Neoceratodus* the olfactory bulbs are pedunculated, and considered that this is the primitive condition for lungfishes. This is undoubtedly correct, because all Gogo lungfishes and as well as *Dipnorhynchus* and *Speonesydrion* specimens are pedunculated. In other words, the best known Devonian species in which the snout region is well known have pedunculated olfactory regions. This is correlated with their expanded snouts containing a large number of tubuli overlying the large olfactory bulbs.

Telencephalon. As we have indicated for *D. sussmilchi* (Campbell & Barwick, 1982: fig. 25a), the floor of the telencephalon drops slightly to the rear of, and also constricts laterally, posterior to the ends of the olfactory canals (Figs. 1B, 4B). Northcutt (1987: 281) commented that in living dipnoans there is a distinctly expanded floor on the telencephalon. In dipnorhynchids any expansion of the floor of the braincase is barely perceptible. Similar comments can be made about the floor of the telencephalon in the Gogo dipnoans, and presumably this is a feature of primitive dipnoans.

A shallow depression, which is too small to photograph in such a secluded position, lies on each side of the midline in the floor of the telencephalon of *D. kurikae*. At the anterior end of each groove is a foramen, and this passes anterolaterally presumably into a tube. We have not been able to see where it emerges. Of particular interest is the entry into the right foramen by four small holes; but on the left a single perforation is present. The function of these structures remains unknown.

The dorsal surface of the telencephalon is not preserved in either specimen. However the shape of the lateral and anterior walls indicates that it was raised above the level of the more posterior parts of the braincase. We cannot determine the extent to which it was divided medially.

Diencephalon. Behind the telencephalon the walls of the diencephalon swell slightly laterally, and ventrally they drop to a point where the base of the foramen for the *opticus* N II makes its exit (Fig. 4). The optic nerve passes from the braincase via a bone-lined tube and an external foramen 5 mm in diameter and oriented mainly anterolaterally, but also a little ventrally. This is similar to the orientation shown by Campbell & Barwick (1983) but unlike that shown by Thomson & Campbell (1971: fig. 32) for *D. sussmilchi*. The optic foramen lies immediately behind the point where the preorbital wall meets the lateral wall of the braincase.

In extant dipnoans the *opticus* N II passes out dorsal to the base of the braincase, and generally it is smaller than that of *Dipnorhynchus*. In *Chirodipterus* and *Holodipterus* the *opticus* canal emerges from the base of the braincase, though in both these genera its point of exit is further forward than in *Dipnorhynchus*. The position of the nerve in these Devonian forms indicates that they display the primitive condition for dipnoans. In *Diabolepis*, the nerve II is situated in a forward position, and the nasal capsule forward of it is also short (Chang, 1995: figs. 5, 11). This interpretation is supported by the position of the orbit as shown by Chang (1995: fig. 2). Other differences between *Diabolepis* and dipnoans, such as the massive differences in the posterior of the skull, are dealt with in a paper that we have submitted for publication.

Behind the *opticus* nerve foramina, the floor of the braincase rises slightly to form the front edge of a commodious hypophyseal cavity. In this rise is a deep median groove that runs posteroventrally down into the hypophyseal pouch. The pouch swells laterally and posteriorly. The pituitary vein passes out laterally and slightly posteriorly within this pouch, and emerges into a large cavity (the *foramen sphenoticum minus*) in the lateral wall of the braincase medial to the conical palatal process

(Fig. 4). The jugular vein runs from a posterior position and opens through the *foramen sphenoticum minus* slightly behind the pituitary vein. The anterior ophthalmic artery passes anteroventrally to the pituitary vein and opens low down on the lateral wall of the braincase just dorsal to the palate. The external opening for this artery is clearly visible on both sides of the specimen, but its internal opening is concealed. Presumably the internal carotid enters the posterior swelling though we have not been able to establish this point. Posteroventrally the hypophyseal pouch passes down into a long narrow buccohypophyseal canal, that opens into the mouth almost at the posterior end of the pterygoid dental plate.

Internally within the braincase, *oculomotorius* N III, is situated 2–3 mm above the anterior wall of the pituitary hypophysis. It leaves the braincase through a foramen that is only 1 mm in diameter, and passes ventrolaterally into the orbital chamber, opening about 7 mm posterior to the optic foramen.

As usual, the *trochlearis* N IV is situated high on the wall of the braincase, and in this specimen is represented on each side by a notch on the upper edge of each side of the neurocranium (Figs. 3, 4). With the palate held horizontally, this foramen is slightly anterior to a line dorsal to foramen for *oculomotorius* N III. It is oriented anterolaterally from the inside outwards.

Mesencephalon and metencephalon. Behind the hypophyseal foramen, the floor of the braincase is almost horizontal except for a broad slight median ridge along its length. The foramen for the moderately large *trigeminus* N V lies well down on the wall, and leaves the braincase about 12 mm behind the hypophyseal pouch. It is entered by a short groove which starts anteriorly. Within a couple of millimetres after leaving the inner perichondrium the tube splits; a thin tube that carried the *profundus* V_1, being directed forwards and downwards to open through the external neurocranial wall in the *foramen sphenoticum minus* on the left side of the specimen (Fig. 4B), but through a small foramen behind that structure on the right side. This nerve is in an appropriate position to run through the floor of the orbital cavity, and thence forwards to the sensory region of the snout. A second much larger tube runs posterolaterally to open through the *foramen sphenoticum majus* (Fig. 4A,B). This carried both V_2 and V_3, which serve the maxillary and mandibular rami.

On the internal surface of the braincase, dorsal to the foramen for *trigeminus* N V, a shallow groove runs upwards, but the specimen does not show any foramen at its top. This, presumably, is the result of erosion of the top of the braincase through weathering.

The wall of the *sphenoticum minus* is a coarse open structure (Figs. 3, 4A), rather than being a continuous layer. Immediately in front of the ventral edge of this structure is a small opening for the anterior ophthalmic artery, described above. Between this foramen and around the *opticus* N II foramen, the wall of the external endocranium is depressed and crinkled. A similar feature is found on some specimens of *D. sussmilchi*.

Examination of the structure of extant dipnoans *Neoceratodus* and *Protopterus* (Northcutt, 1987) shows that the *facialis* N VII and the *accousticus* N VIII leave the wall

of the braincase close behind nerve V; in addition, a branch of the anterior lateral line nerve passes out dorsal to nerves VII and VIII. The two new specimens of *D. kurikae* do not show any exits close behind nerve V, and the interpretation of the existing foramina have to be understood in terms of general principles. We reached the following conclusions.

In the inner perichondrium about 7–8 mm posterodorsal to the *trigeminus* N V foramen, is a vertically elongated foramen which runs laterally into a foramen in the top of the *foramen sphenoticum majus* on the left side, and to a small foramen dorsal to the same position on the right side. This structure is in an ideal position for the *anterior lateral line* nerve (Fig. 4B). Its position can be compared with that of *Neoceratodus, Protopterus* and *Latimeria* as illustrated by Northcutt (1987).

In the internal wall immediately below the above foramen, a shallow but wide groove runs into the front wall of the utriculus, and then runs posterolaterally into the thick neurocranial wall. Within the wall the tube splits into two, the dorsal one of these emerges in the dorsal extremity of the *foramen sphenoticum minus*, and probably carried the *superficialis ophthalmicus* N VII. The ventral one enters a long tube that runs postero-ventrolaterally to open through the *foramen prooticum basicraniale* along with the jugular vein. It must therefore be the *hyomandibularis* N VII.

Posterior to where the *facialis* N VII leaves the braincase, the walls expand laterally to form the inner face of the otic region. At the anterodorsal end of this expansion, incomplete gaps in the specimen show where nerves open out of the braincase and pass laterally through the thick lateral walls. This must have been for the nerve *accousticus* N VIII. Its course is not preserved but it must have turned into the otic region after a short distance. We assume that the brain stem maintained a linear course through this region, and we have so represented it on Fig. 4B.

The walls of the braincase turn downwards in front of the otic region, and the anterior end of the notochordal chamber penetrates this wall for about 3–4 mm. This puts the end of the notochordal chamber anterior to the level from which the nerve *accousticus* N VIII passes out.

The second specimen, ANU 48678, shows the otic region moderately clearly, except that the vertical semicircular canals are missing. Figure 5A shows the specimen with the outlines of the canals and the otic region drawn onto it, and Figs. 5B and 5C are reconstructions of the soft tissues inferred from it. The right side of the specimen has been weathered, exposing the internal structure of same. The left side has been not so deeply weathered but exposes the horizontal part of the semicircular canals. This gives sufficient information on the general structure of the region to be able to reconstruct the overall pattern.

The posterior part of the notochordal chamber has also been lost allowing observation of the sacculus, the utriculus, and the superior sinus. In addition this specimen shows the position of nerves N VII to N X more clearly than any other Early Devonian form. The utriculus is large and extends across the anterior face anterodorsally to the terminus of the notochord, and it is crossed by the *facialis* N VII as has been described above. The *accousticus* N VIII is dealt with in the section below dealing with the semicircular canals.

Nerve *glossopharangeus* N IX is known only from its exit from the posterior part of the sacculus, which is its standard position on Devonian dipnoans. It passes out in a lateral direction.

The passage of nerve *vagus* N X is preserved as a groove passing below the posterior part of the superior sinus of the saccular cavity, and then parallel with the ventral edge of the ampulla for the posterior semicircular canal. It passes out of the bone in a posterolateral direction.

The horizontal semicircular canal is not evenly curved, its external edge being almost straight. Its external ampulla lies well behind the anterior end of a transverse line through the superior sinus of the saccular cavity. Below the external ampulla it turns ventrally into the sacculus. Posteriorly the horizontal semicircular canal maintains its width throughout its length, and passes into the posterior end of the superior sinus of the saccular cavity. At the posteromedial corner the horizontal canal is connected with the marked swelling that represents an ampulla at the base of the posterior vertical semicircular canal. This is the largest ampulla of all three preserved, and anteriorly it joins via a large foramen into the posterior part of the superior sinus. This foramen provided entry for a ramus of the *accousticus* N VIII. The posterior semicircular canal that must have arched from this ampulla to the top of the superior sinus, would have been aligned at a low angle to the axial plane. The anterior vertical ampulla is connected with the horizontal canal as expected, and it also opens down into a foramen opening into the top of the sacculus. This must have carried a branch of nerve N VIII. As well as opening into the horizontal canal, this ampulla must have opened directly into the superior sinus of the saccular cavity, but this part of the specimen has been lost during preservation. We have reconstructed the canal so as to give a functional orientation with respect to the posterior canal.

The sacculus, which is exposed on both specimens, is large and has a convex well-rounded base extending ventrally to the base of the notochordal canal. The lateral wall has a very oblique surface sloping ventromedially at about 45°. The lateral margin is sharp and lies almost at the point where the jugular vein passes through the posterolateral wall.

Neither specimen has the anterior or posterior semicircular canals preserved, and we have no direct means of determining the height of the superior sinus. We do know, however, that the roof of the other dipnorhynchids is high and is supported from the braincase on a high median septum and two high dorsolateral septa. One skull roof of *D. kurikae* has the dorsolateral cristae partly preserved, and they are in a lateral position as in *D. sussmilchi* rather than close together as in *Chirodipterus australis*. This implies that the vertical space for the superior sinus or the space for the *ductus endolymphaticus* is large. Consequently we have restored these structures to the height implied by the space available from the horizontal structures that are preserved.

The only Devonian species with which a comparison of the labyrinth can be made are *Chirodipterus australis* Miles, *Holodipterus gogoensis* Miles and *Griphognathus whitei* Miles from the Late Devonian at Gogo, and *C. wildungensis* Gross from the Late Devonian of Wildungen. Säve-Söderbergh's (1952) attempt to understand the Wildungen specimen depended on his destruction of the specimen with a hammer and chisel. His illustration (1952: fig. 9, pl. 5,

fig. 4) of the otic region shows a clear outline similar to that given by Miles (1977: figs. 47–48), but the horizontal semicircular canal is not present on his photograph and is reconstructed on fig. 9. Despite this incompleteness, the two species of *Chirodipterus* are very close indeed. Neither of these species has the large ampulla on the posterior semicircular canal, the large utricular recess, and the laterally compressed horizontal canal, as found in *D. kurikae*. In *Chirodipterus*, the horizontal canal is semicircular in outline in dorsal view. *Holodipterus* is discussed by Miles and is said to be close to that of *Chirodipterus*. *Griphognathus whitei* has a similar arrangement to that of *Chirodipterus*, but its proportions are different because of the flattened shape of the skull. These differences are small in comparison with the obvious similarities between the species, and its occurrence in all the Devonian species in which the labyrinth is preserved, leads us to conclude that it is the primitive dipnoan pattern. Details of the comparison between the otic region of primitive dipnoans was discussed by Miles (1977: 98–103).

The nasal capsule

The capsule is preserved on the left side cf. ANU 48676, and is quite uncrushed. Miles (1977: 123) commented on the Gogo dipnoans that the surface of the neurocranium was evidently without a perichondral bone layer. The dorsal view of this specimen shows the junction between the dermal bone and the endocranium, and a perichondral layer lies around the endocranium (Figs. 3, 6A). We have also observed a similar layer in *C. australis*. The boundary between the neurocranium and the dermal bone is clearly outlined, and it is exactly like the boundary between the neurocranium and the dermal bone of the palate illustrated by Campbell & Barwick (1985: fig. 6d). The tubules over the top of the capsule, that is in the ethmoid capsule, were situated in a cartilage matrix (Miles, 1977: 133).

An internasal septum (*septum nasi*), is narrow and rather sharp crested towards the rear, but fades away almost completely anteriorly (Fig. 6B). It is formed of endocranial
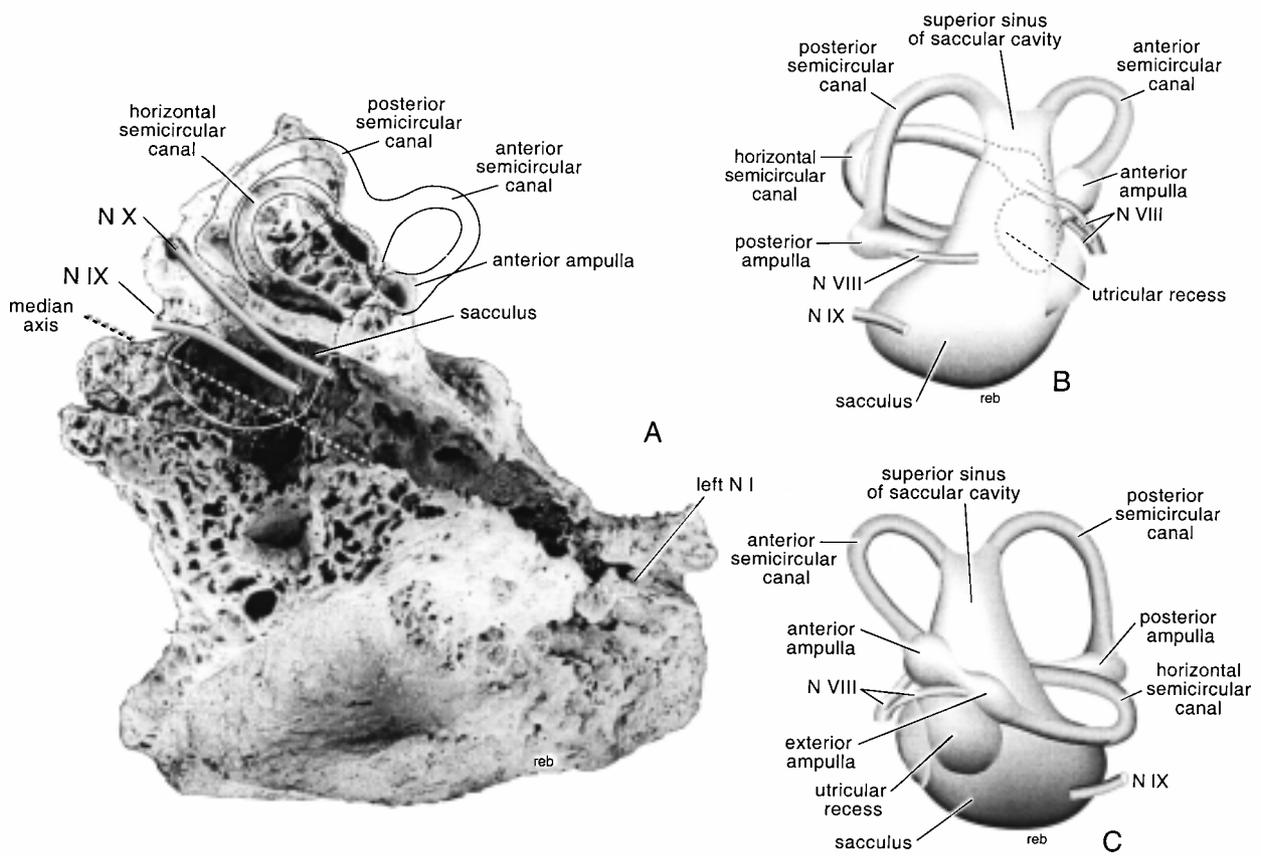

Figure 5. *Dipnorhynchus kurikae*. A—dorsolateral view of ANU 48678, the same specimen shown on Fig. 2. The semicircular canals were stripped off during preservation, but the details of the superior sinus of the sacculus, the ampullae of all three canals, and features more ventral to it are preserved. The height of the superior sinus is restored according to the height in the dorsolateral process supporting the braincase. The median axis is drawn along the base of the braincase. B—reconstruction of the left otic region viewed from the medial side. Outlines of structures on the lateral side are dotted. The same viewed from the lateral side. Nerve VIII is based on a canal and foramina in the specimen, and nerve IX is based on a foramen in the posterior wall of the specimen behind the sacculus. Scale = 10 mm.
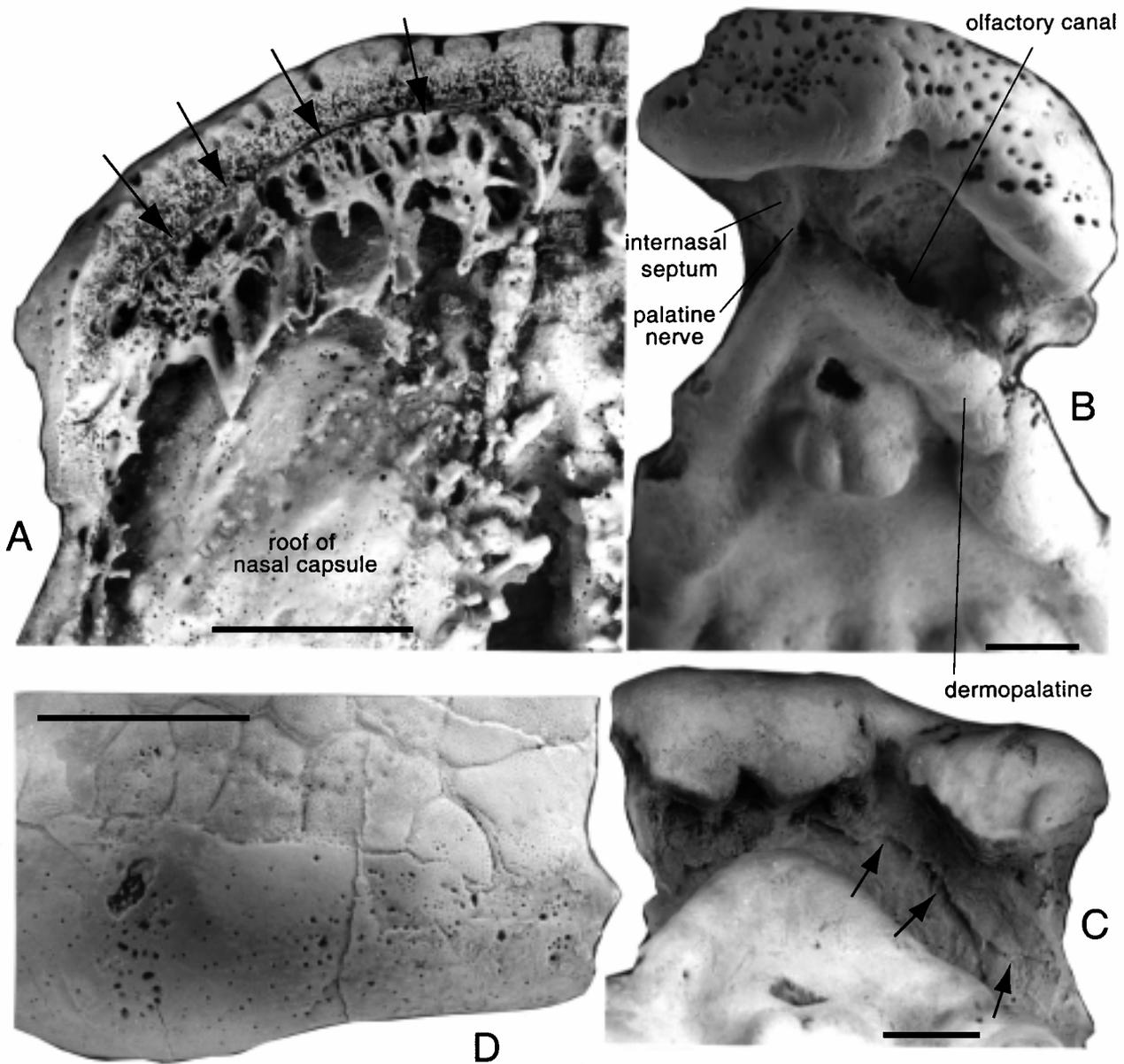
Figure 6. *Dipnorhynchus kurikae*, A–C from ANU 48676. A—dorsal view of the nasal capsule and snout, showing the dermal bone (innermost boundary arrowed) with pores in the outer layer, the gap between the dermal bone and the neurocranium with no tubules crossing into the dermal bone. The roof of the nasal capsule shows few structures because it was largely removed during preservation, and the black spots on it are bubbles in the impregnating plastic. B—view of the palate and snout with the snout tilted towards the observer. In the snout, note the pores some of which are in groups, the perforations for the palatine nerves, and the opening of the olfactory canal. C—same specimen tilted in the opposite direction, showing the flattened surface without pores on the inside of the snout, and the boundary (arrow) between the roof of the nasal capsule and the dermal bones of the snout (arrowed). D—*Dipnorhynchus sussmilchi*, anterior end of the snout of ANU 18815 showing the hard surface lying in front of the cosmine-bearing plates, the course of the lateral line canals, and the small pores on the anterior surface. Scales = 10 mm.

material, and its surface is smooth without any evidence that it continued ventrally as cartilage. Unlike *Chirodipterus australis*, it has no flattened surface to which a palatal bone (identified as a vomer by Miles) was attached. This is as would be expected, as the so-called vomer lies in a more posterior position between the dermopalatines in this species, and in comparison with *C. australis* the *septum*

nasi certainly has a curious appearance (Miles, 1977: 134–135). Beyond its anterior end of the *septum nasi*, the edge of the anterior lip has a pronounced embayment within which is a foramen. This and foramina under the projections forming the embayment apparently connected with the tubules in the ethmoid capsule.

The nasal capsule is divided into three recesses (Fig. 7), which were discussed for *D. sussmilchi* by Thomson & Campbell (1971: fig. 29), whose terminology we use herein. The largest and deepest recess is posterior and it lies partly covered by the palate. The anteromedian recess is smaller than in *D. sussmilchi*, lies against the *septum nasi* medially and terminates against the anterior lip. The anterolateral recess is not sharply separated from the posterior recess, and anteriorly it runs up to the inner margin of the anterior naris. The anterior naris, which makes a deep recess in the anterior lip (Figs. 1A, 6B,C), connects with a shallow groove on the *solum nasi* which runs posteriorly across the anterolateral recess to the posterior recess. Miles (1977: 135) commented that he did not consider the threefold subdivision to be of significance, largely because no threefold division is present in *Chirodipterus australis*. On the other hand, it is present in *D. kurikae* in the same way as in *D. sussmilchi*, and clearly it is a feature of *Dipnorhynchus*. Bartsch (1993) commented that the outbulgings of the nasal sac present in early growth stages in *Neoceratodus* do not maintain their positions during ontogeny, and one suspects that outbulgings such as those in *Dipnorhynchus* represent the adult series of structures lost in later genera.

In dorsal view the olfactory tract has furrows in the surface indicating that the internal structure is complex. The olfactory tract expands in width and enters the posteromedial corner of the olfactory recess. In addition this recess is entered by two tubes, one lying close to the olfactory canal, and the other being a little more laterally placed (Figs. 3, 4A, 7). The former is much smaller than the latter, which is the opposite of the illustrated situation in *D. sussmilchi* (Thomson & Campbell, 1971: fig. 29). The interpretation of these canals is difficult, but we consider that the larger canal contained the *ramus maxillaris* N V_2, and the smaller one the *ramus ophthalmicus profundus* N V_1. The bone forming the roof of the nasal capsule is thin and was partly exposed by weathering. The exposed surface has numerous foramina which originally opened into the tubules in the ethmoid capsule. Thomson & Campbell (1971: fig. 29) show three canals running out of the dorsal surface and connected to the *olfactorius superficialis* N VII at the posterior end. We cannot confirm that a foramen for that nerve occurs in *D. kurikae*. However, two canals exit the capsule, one in a median position and the other laterally, at the front of the posterior recess (Fig. 1B). These canals join up with the tubules in the ethmoid capsule. Their connections are not clear.

Two other structures of consequence are present. The *palatine* N VII nerve exits from the palate in the appropriate position at the end of the palate. The groove for the subnasal vein (*maxillaris* vein of Miles, 1977) is in its usual position for Devonian dipnoans.

What appears to be part of the infraorbital lateral line canal runs along the lateral part of the specimen just dorsal to the edge of the labial pit (Fig. 1D). It is broken and cannot be traced around the anterior margin, though fragments are preserved. Anteriorly it is deeply buried in the bone and no exit pores have been observed. No part of the supraorbital canal is preserved.

The snout

An obvious feature of *D. kurikae* is large number of pores in the snout (Figs. 6A,B, 8A,B), these being more than three times the diameter of the largest pores in *D. sussmilchi*. The outline of the labial pit is preserved on the left side of the individual. It is much higher than the pit on *D. sussmilchi* (Fig. 1D). Both species of *Dipnorhynchus* have more laterally directed labial pouches which are more voluminous than those of *Chirodipterus australis*. This fits well with the fact that the mandible also has a large forwardly placed labial pit (Figs. 9C, 10A,B) that matches the large pit in the snout. The specimen also has the advantage of being weathered through the snout region so any interrelationships between the pores and the underlying bone can be observed.

Large pores are scattered over the anterior face of the snout, the largest ones being at the anterior edge (Figs. 1D, 6A,B). These reach a maximum diameter of about 1.5 mm. Some of them are not single units but are split internally into two or three elements. The smaller pits are limited in number to a few in a small cluster dorsal to the left nostril— they are only 0.3 mm in diameter. The returned margin of the lip, which turns back towards the nasal cavity, has no pores at all, and the small pits in this position on Fig. 7 are gaps in the impregnating substance. This returned surface is large in comparison with comparable surfaces on *D. sussmilchi* and *Chirodipterus australis*. Because it had distinctive bottom feeding characteristics with an extended bottom-feeding snout, *Griphognathus* had a much larger surface in this position.

At only one point, immediately dorsal to the labial pit, does the coarsely porous bone of the snout pass backwards into the pores of the cosmine surface (Fig. 1D). The boundary between the two types of surface is sharp, there being no place where the cosmine pores lie between the larger pores. On the other hand, the larger pores become smaller towards the cosmine, though they remain scattered and are still much larger than the cosmine pores.

The worn section across the snout (Fig. 6) shows several features that are distinctive. The outer layer, named layer 1 herein, is up to 2.5 mm thick. It is formed by columns of crystals with their long axes arranged normal to the specimen surface, and are separated by thin gaps—they can be observed by direct observation of the specimen, or by thin sections (Fig. 8). The hard material contains no dentine tubules, demonstrating that it is not dentine. The composition of the crystals will be discussed below. The crystals around each tube all go to cross-polar extinction in approximately the same position and there is little doubt that they are oriented in the similar direction. The space between the hard tissues consists of vertical calcite filled tubes. As can be seen in thin sections, these canals branch especially towards the outer surface. Despite this, the layer of tissue is hard and obviously withstood wear.

Inside this outer layer is a more vesicular bony layer, named layer 2 herein, which merges into layer 1. The boundary is clear at all levels of observation because in the inner layer the canals are more or less vertical, but are less regular in orientation and are more widely spaced (Fig. 8A,B,D). Some of the canals in this layer are continuous
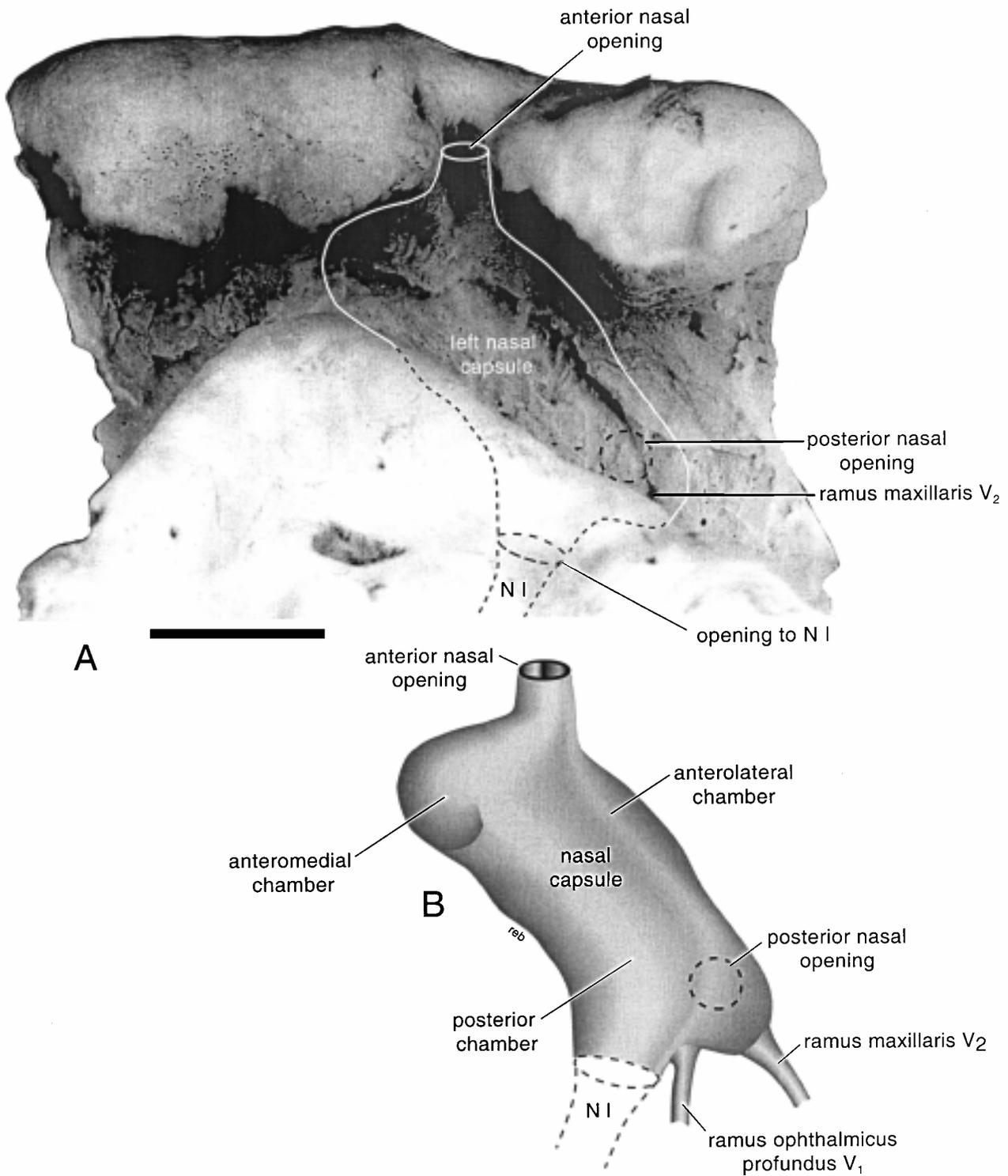
Figure 7. *Dipnorhynchus kurikae*. A—ANU 48676, tilted to the right, and with the anterior edge downwards. Outline of the nasal capsule inferred, and posterior nasal opening inferred from the shape of the dermopalatine. Position of the nerve N I observed and is so far under the palate because of the tilt on the specimen. B—reconstruction of the nasal capsule which does not have the strong subdivision as shown by Thomson & Campbell (1971: fig. 29), which was drawn from ANU 18815. Scales = 10 mm.
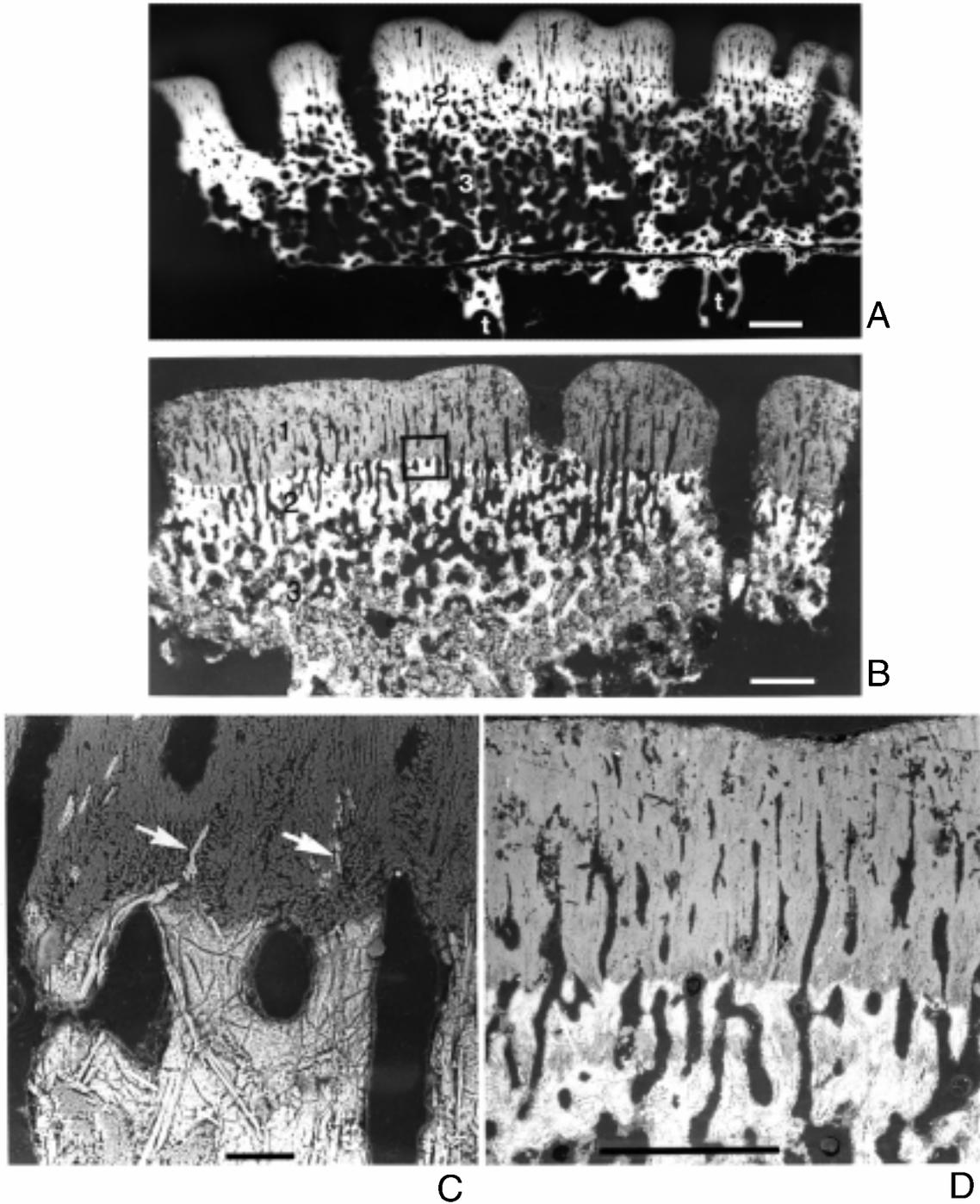
Figure 8. *Dipnorhynchus kurikae*, structure of the upper lip of ANU 48676 in both thin section and SEMs. A—thin section photographically printed directly from the slide, cut from the edge shown in Fig. 6A. Note the outer layer labelled 1, with its inner edge marked by a line of small perforations. Layer 2 has less regular canals and passes into layer 3 which consists of vesicular bone. The large outer pores vary in depth according to the orientation of the section. The boundary between the dermal bone and the neurocranium is marked by the two parallel bone layers. Fragments of tubules are labelled t at the base. B—SEMs of an adjacent layer which does not pass through so many pores. Layer 1 has a dark colour, the result of silicification, which was the result of preservation. Layer 2 shows many vertical canals passing into layer 1. The lower part of the section, including the lower part of layer 3, has calcite infilling. C—enlargement of the area in the rectangle showing crystals of fluorapatite at the base, and columns of quartz at the top. Note the fragments of apatite remaining in the quartz (arrowed). D—a wider area around the rectangle shown in B. Note the irregular arrangement of crystals in the lower columns. Scales: A, B and D = 1.0 mm; C = 0.1 mm.
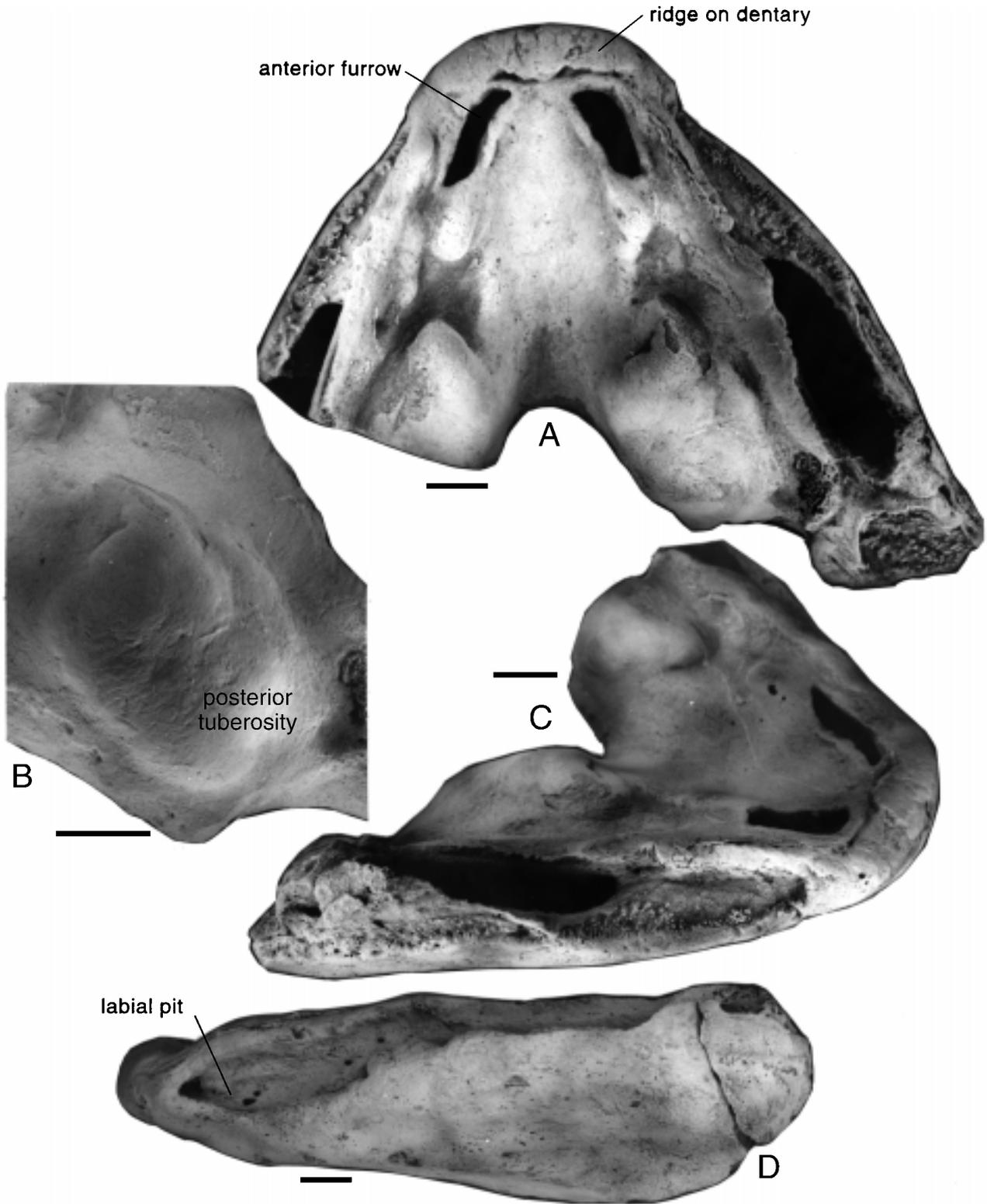
Figure 9. *Dipnorhynchus kurikae*, A–C from ANU 35643. A—dorsal view of a mandible from which the sections in Figs. 15A–C were cut. Note the shapes of the posterior tubercles, the glenoid fossa, the granules along the top of the surangular. B—an enlargement of the posterior tuberosity tilted to show the shapes of the different parts of the surface. C—anterolateral view of same specimen. Note the shape of the labial pit, the granules along the surangular, the low ridge on the dentary, and the rounded shape of the posterior tuberosities. D—lateral view of the ANU 60030. Other views as on Figs. 11, 12. Scales = 10 mm.
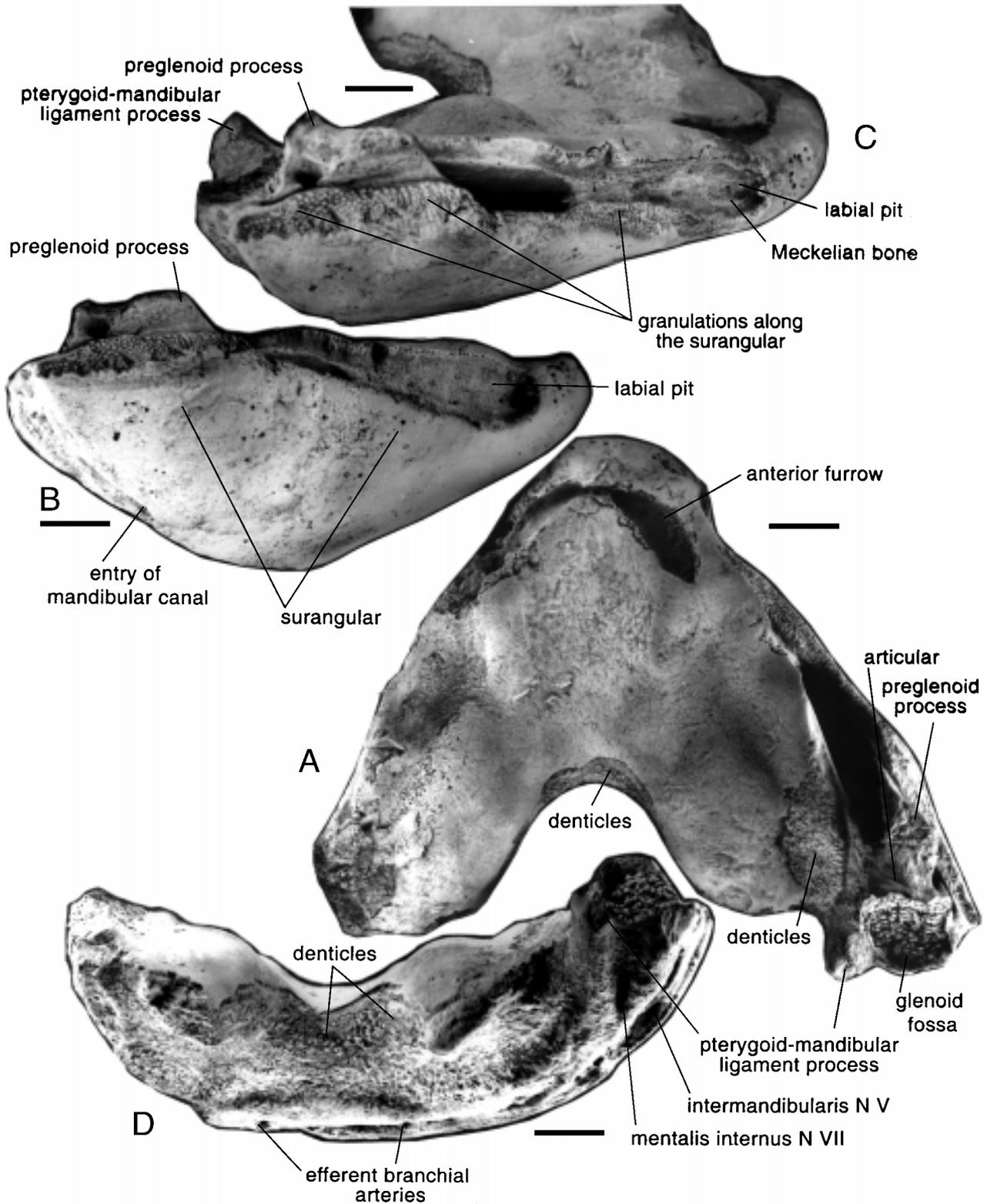
preglenoid process

pterygoid-mandibular
ligament process

C

labial pit

Meckelian bone

preglenoid process

granulations along
the surangular

labial pit

B

entry of
mandibular canal

surangular

anterior furrow

articular

preglenoid
process

A

denticles

denticles

glenoid
fossa

denticles

pterygoid-mandibular
ligament process

intermandibularis N V

mentalis internus N VII

D

efferent branchial
arteries

Figure 10. *Dipnorhynchus kurikae* ANU 60028; four views of a well-preserved mandible showing details of the right side clearly. A—dorsal view showing the slight secondary swelling of the glenoid fossa, and the preglenoid process. B—lateral view of same showing the large labial pit with the down-turned lateral edge on the surangular along its margin, and the denticles along the edge of the dental plate. C—oblique view of same showing the very high pterygoid-mandibular ligament, the large preglenoid process, the very high surangular along its lateral edge, the strong granulation along the surangular lateral to the labial pit, and the absence of large nerve pores in the posterior part of the pit. Note also the edge of the surangular and its junction with the outturned edge of the prearticular to form the base of the posterior part of the labial pit. Anterior edge of labial pit with pores in Meckelian Bone. D—posterior view of same showing the posterior end of the dental plate, the foramina for the nerve intermandibularis V; a groove running along the boundary between the articular and the prearticular and ending in the foramen for the mentalis internus N VII; and the foramina for the efferent branchial arteries symmetrically placed on either side of the mid-line. Scales = 10 mm.

with those in the outer layer. SEMs show that this layer is made of coarse crystals some of which are oriented normal to the surface, but others meet them obliquely (Fig. 8C,D).

Layer 2 merges gradually into layer 3 in which the vesicles are more equidimensional and the bone is more open. Internally the open spaces in the bone become more irregular, and its inner edge is formed of a very thin sheet of membranous bone.

The pores in the outer wall penetrate layer 1, and terminate within layer 2 (Fig. 8A,B). Those that terminate in layer 1 in thin sections appear to do so because of the obliquity of the section. No secondary pores have been observed entering the pores either at their base or laterally.

Inside these three dermal layers is a narrow gap bordered by thin membrane bones (shown by black arrows in Figs. 6A and 8A). Inside that are the branching tubules which are connected to the nerves V and VII which normally occupy tubules in the ethmoidal capsule. The tubules branch rapidly towards their termini (Fig. 6A), and they end abruptly against the gap between the membrane bones described above. Nowhere is there evidence that the tubules cross into the dermal layers, and neither is there evidence that the external pores in the dermal bones are in any way served by the nerves in the tubules.

From the external surface other aspects of the pores have to be taken into account. Some of them are not single structures, but consist of groups of two or three pores (Fig. 6B). Others are in small clusters. Finally as Figs. 8A and 8B indicate, the external entrance to the pores curve uniformly into the pores, suggesting that the soft tissues on the external surface dropped evenly into the pores.

Interpretation of dermal structures of the snout

The three layers described above are obviously parts of the dermal bone. X-ray diffraction study of layer 1 shows that it is composed of quartz and fluorapatite. The arrangement of these minerals is shown in Fig. 8C,D, and their distribution has several features of significance. The inner boundary of layer 1 is relatively straight against layer 2, and it crosses the vertical canals no matter what their orientations are (Fig. 8B–D). Sections along the boundary of layers 1 and 2 indicate that there is a sudden break between the tissues in any one column. Also included within this layer are crystals seemingly of material like that of the layer 2. From an optical mineralogical investigation and an SEM study of composition, we have concluded that layer 1 was originally apatite, but it has been replaced by silica, and fluorapatite. Immediately we are faced with the possibility that the replacement has removed dentine tubules, but we conclude that this is not correct. SEMs show no sign of the remnants of such canals, and the presence of cosmine pores in the adjacent surface indicates that fine structures have been preserved.

Analysis of layers 2–3 indicates that they are composed of fluorapatite, and the crystals are irregular in their orientation.

The external surface must have been covered with an epithelium, and the pores on the outer wall must have been filled with material related to the epithelial structures.

Although the possibility remains of some fine connections with the internal layers, it is probable that the pores contained special surface structures such as mucous glands, and are not related in any way to endocranial tubules.

Other possibilities remain to be considered, largely following on the work of Bemis & Northcutt (1992), based on *Neoceratodus*. These authors also made comparisons between the *Neoceratodus* and some Devonian forms such as *Chirodipterus australis, Holodipterus gogoensis* and *Dipterus valenciennesi*. We are reluctant to make comparisons between *D. kurikae* and these species because the bone in their snouts consists of dentine in which the flask chambers of cosmine can be seen. There is no evidence that the dermal bone in these species has structure like that described herein for *D. kurikae*. In *Neoceratodus*, the dermal layer gives rise to dermal papillae and ampullary organs which are irregularly distributed. Neither of these features has the appearance or orientation of pores in the dermis of *D. kurikae*. Consequently we are not convinced that these features displayed by *Neoceratodus* can be appropriately recognised in *D. kurikae*.

We have also examined the two skulls of *Dipnorhynchus sussmilchi* available to us. The bone with the cosmine pores stop suddenly along a surface line (especially on ANU 18815), and anterior to that the bone is hard and contains no cosmine, but it does contain the pores for the lateral line canals (Fig. 6D). Larger more irregularly arranged pores occur across the remainder of the rostral area—they are quite comparable with the pores on *D. kurikae*, though they are much smaller. We have no explanation of the significance of size differences. It seems that the presence of pores is a characteristic feature of *Dipnorhynchus*.

The mandibles

External dermal bones. We now have four mandibles of the species, whereas at the time of original description we had one fragmentary individual, and another more or less complete one. With the specimens arranged so that the ventral median edge is horizontal, the smallest is 83 mm long, and the largest is 143 mm. The original specimen is 100 mm long, not 92 mm as stated in 1985. The range of sizes gives us an opportunity to discuss the ontogeny of the species. Now we describe the main features.

The mandible is low as is reflected by the posterior profile (Fig. 10D). The dentary increases in relative width compared to the total width of the specimen, being 0.27 in the smallest and 0.37 in the largest. Some specimens, especially one of the type specimens, have a shallow furrow on the ventral surface running transversely from the front end of the labial pit in an arc to the midline (Campbell & Barwick, 1985: fig. 8b). A complimentary furrow occurs on the other side. This marks the posterior edge of the dentary. Other specimens have a weaker furrow which is sometimes difficult to detect.

On the dorsal face of the dentary is a well-rounded ridge which is poorly developed on the smaller specimens but is high on the larger ones (Figs. 11A, 12, 13A,B). The ridge is not complete in all specimens, but in some it is divided into two or three irregular lobes (Figs. 9D, 13A,B). The best
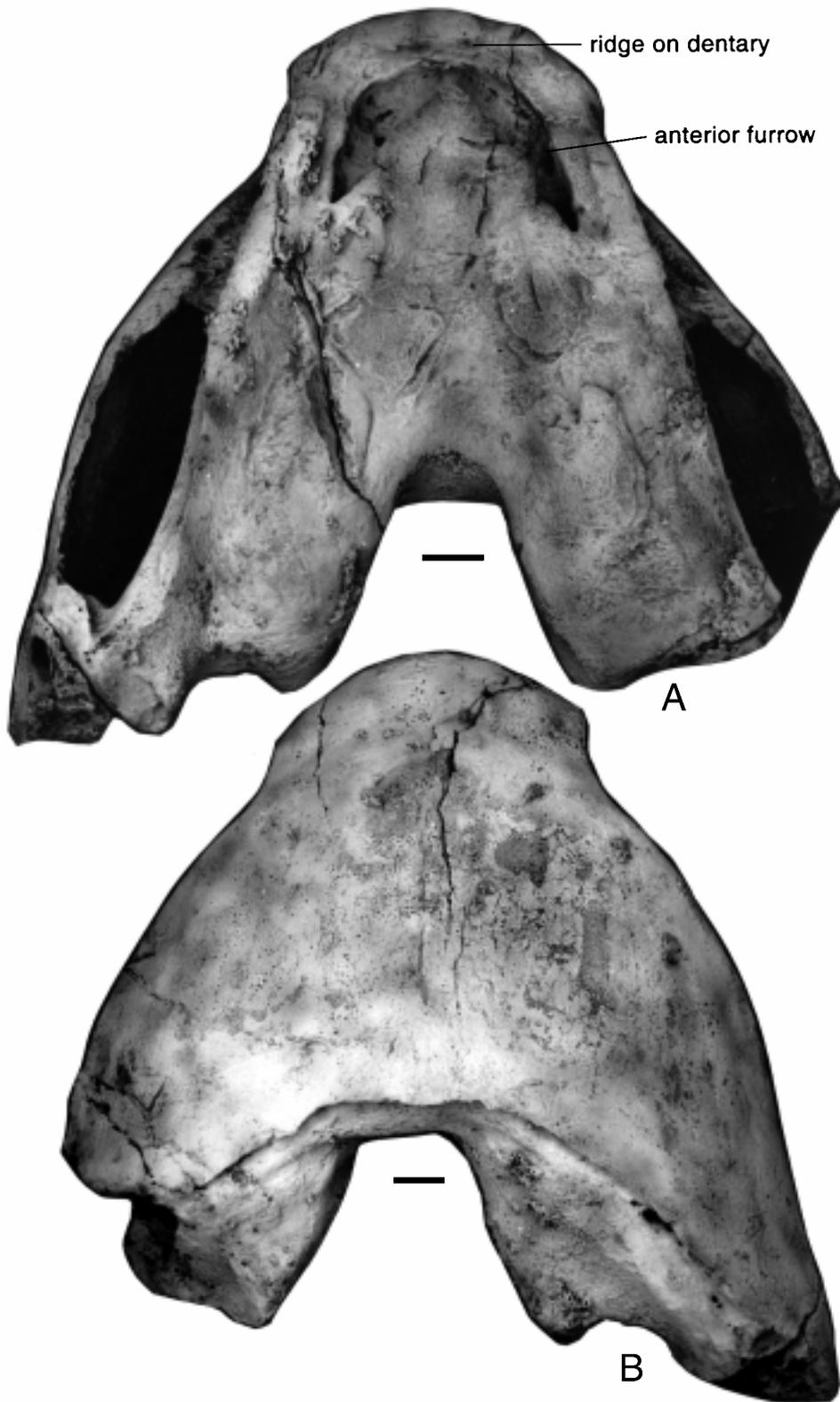
Figure 11. The largest specimen of a mandible of *Dipnorhynchus kurikae* known in ventral (A) and dorsal (B) views, ANU 60030. Details are labelled on Fig. 12. Note that the boundaries between the dermal bones are not clearly defined, but are overgrown by cosmine. Scale = 10 mm.
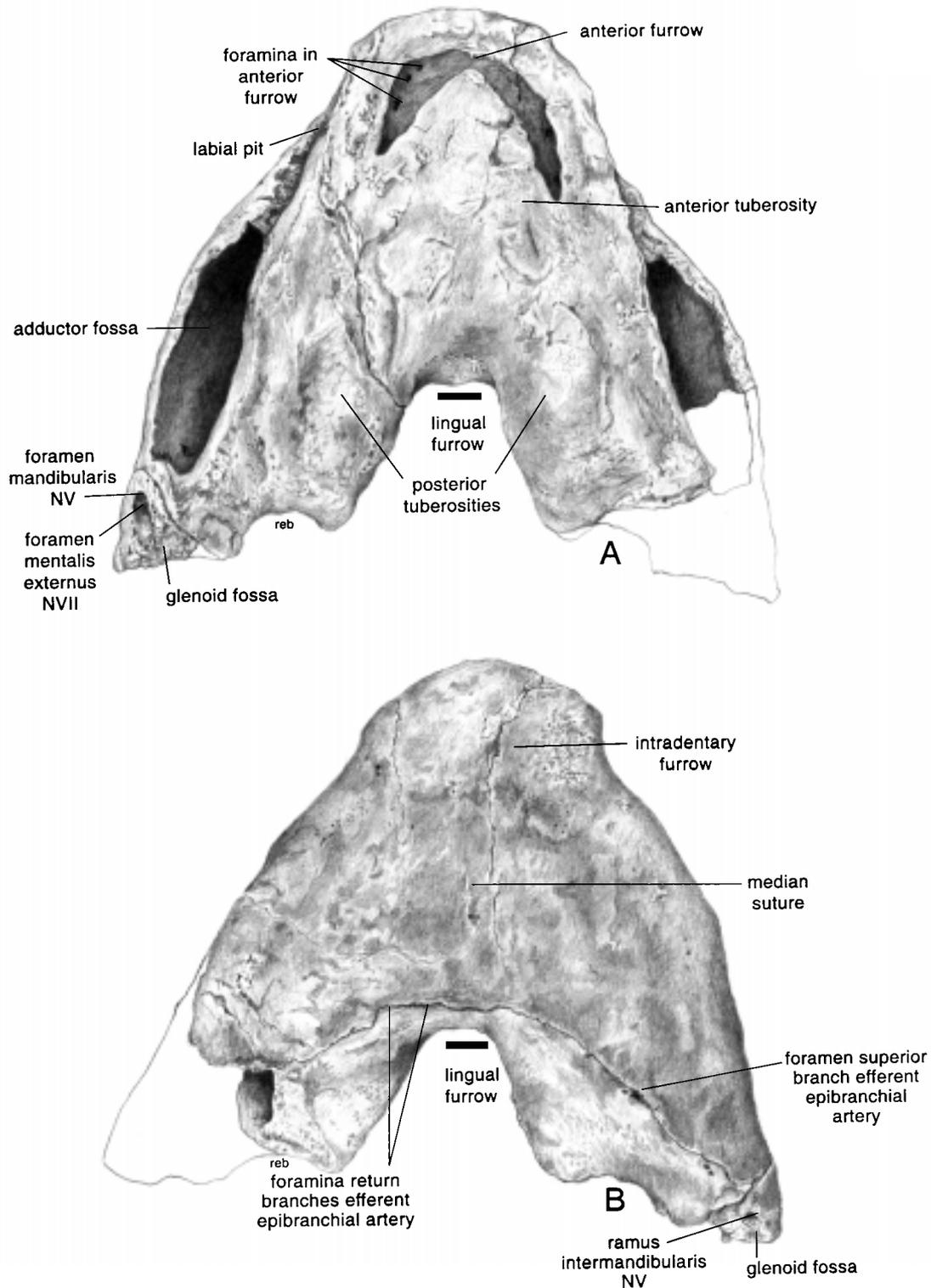
Figure 12. Illustration of specimen photographed in Fig. 11; ventral (A) and dorsal (B) views. Scales = 10 mm.

preserved individual has a break on its right side where the ridge becomes about half the height in the median portion. No pores like those of the surrounding dentary bones are present in the ridge. The edge of the ridge is differently developed on various members of the species. On ANU 60029 (Fig. 13A,C) both anterior and posterior edges are sharp, though the anterior one is less regular. The posterior

edge is not straight but has small posteriorly directed expansions that overhang the dentary. What is more, the contact between the ridge and the dentary is exposed in places as a sharp line. The ridge must have been superimposed on the dentary. Because it becomes larger with age, the new tissue must have been deposited in layers, the mineralisation being supplied through canals running
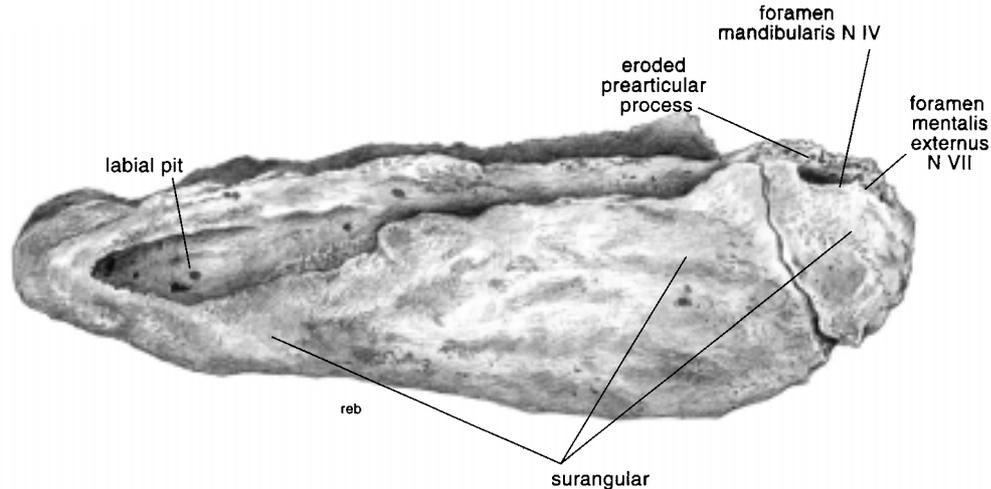
Figure 12 continued. Illustration of specimen photographed in Fig. 11; lateral view. Note that this specimen is depressed in relation to Fig. 10B.

up from the dentary. These canals can be seen in the ridge tissue itself, and it has been sectioned on ANU 60030 (Fig. 14). Details will be discussed below. The anterior edge on the same specimen also has a sharp edge laterally but the median part is broken. On *D. kurikae*, the dentary has no teeth such as those that occur on *Diabolepis* (Chang, 1995), in which the dentary teeth are of the same kind as on the prearticulars though they may not be in line with any rows of teeth on those bones.

The outlines of the infradentary bones are not clear on the specimens, but enough information is available to give a description of the main features. The surangular is a long bone reaching almost to the anterior end of the labial pit, where it comes into contact with the dentary. Its ventral edge is concave medially. Its posterodorsal surface against the articular is without cosmine and is covered with a fine granulation (Figs. 9A,C, 10A,B, 13C). Anteriorly its dorsal edge is inturned and is also covered with granules. It forms the outer half of the labial pit, but it is not upturned to form an outer raised rim to the pit. The posterior boundary of the angular is determined by the position of the mandibular lateral line entering the bone, but its anterior edge is not clear on the external surface of any specimen. Some details can be obtained from the internal view of the external bones provided by ANU 60029 which shows that the angular is a short bone that does not reach to the dentary, and from ANU 35643, which was figured in the original description. The postsplenial and the splenial are long bones which reach to the dentary. The postsplenial has a large lateral extension that turns around the angular towards the surangular ventral to the labial pit. The pattern of infradentaries is similar to that figured by Thomson & Campbell (1971: fig. 18A) for *D. sussmilchi*.

Anterior furrow. As with all other dipnorhynchids, the anterior furrow (Figs. 9A, 10A, 11A) is well developed. It extends extensively posteriorly, and in its floor are several foramina that open into the space ventral to it. We consider that this furrow, which contained well innervated soft tissue and is placed at the entrance to the mouth, is likely to have contained sensory structures (possibly chemosensory) related to food

intake. *Chirodipterus* and probably *Dipterus* both have anterior furrows, and we consider that it is a feature of primitive dipnoans. The anterior furrow is not defined as a gap between the dentary and the prearticulars, but also as a space within which well innervated soft tissue was present. So far as we know, no such furrow which is innervated from the space ventral to it, appears in *Diabolepis* (Chang, 1995).

Labial pit. The labial pit is elongate and is bordered by the surangular. The dorsal edge of this bone does not form an upturned edge to the pit, but is bent downwards. As occurs in all dipnorhynchids, it joins the Meckelian bone to form the posterior floor of the labial pit. In *Chirodipterus*, the adductor pit is sealed off from the labial pit by the Meckelian and angular bones. *Dipnorhynchus* has a similar arrangement, though the surangular rather than the angular makes contact with the Meckelian bone. In both *Chirodipterus* and *Dipnorhynchus*, the anterior floor of the labial pit is made of Meckelian bone. In *Diabolepis*, the adductor pit is sealed off from the labial pit by the Meckelian and angular bones. *Dipnorhynchus* has a similar arrangement, though the surangular rather than the angular makes contact with the Meckelian bone. In both *Chirodipterus* and *Dipnorhynchus*, the anterior floor of the labial pit is made of Meckelian bone. In *Diabolepis*, the adductor pit is joined directly to the so-called labial pit (Chang, 1995: figs. 13, 14). The lateral margin is made of the dentary rather than the surangular or the angular, and so far as we know, the Meckelian bone is not directly turned laterally to form the base of the labial pit. In fact, the whole structure of the labial pit in *Diabolepis* needs further investigation, along with the so-called anterior pit, before comparison with dipnoans is attempted.

Dermal bones on the posterior face. These are well exposed on ANU 35643 and ANU 60028. Most of the surface is made up of the prearticular which is thick and has a rough surface. The articular bone does not have a sharp boundary with the prearticular, but it has an approximate boundary as shown on Fig. 10A. The foramen *intermandibularis* N V is in the usual position, and has a
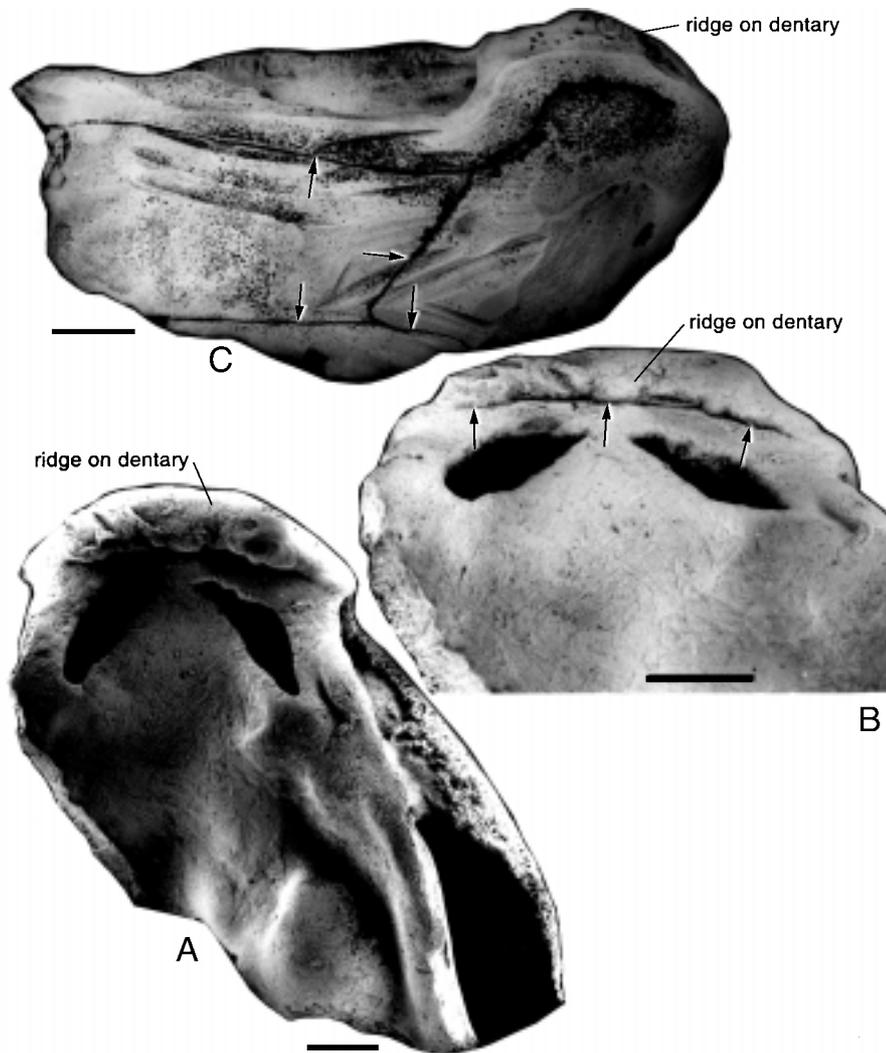
Figure 13. *Dipnorhynchus kurikae*, incomplete mandible ANU 60029. A—dorsal view showing the denticulated edge of the surangular along the edge of the labial pit, and the strong ridge along the dentary. B—posterior view of the dentary showing the nature of the overlap (arrows) area of the ridge on the dentary. C—ventrolateral view of specimen showing the lateral line canals (arrows) revealed by grinding the surface. Scales = 10 mm.

slight groove running both dorsally and ventrally along the boundary between the surangular bone and the articular. A small canal opens through the boundary between the articular and the prearticular medial to the *intermandibularis* foramen in the position illustrated by Thomson & Campbell (1971: figs. 21, 22) as f_1 sa1. This foramen has a vertical groove running into it dorsally. Internally its course can be followed along a canal on the inner face of the prearticular as shown by Thomson & Campbell as indicated above. We consider that it carried the *ramus mentalis internus* N VII. The canal labelled as fV? by Thomson & Campbell is also well shown on ANU 60028, and it rises up the back wall of the adductor chamber to meet the canals as shown by Thomson & Campbell (1971).

Large foramina occur between the angular and the prearticular, but a smaller one on ANU 60028. Unlike *D. sussmilchi*, it seems probable to us that several efferent branchial arteries entered the mandible here.

Lateral line canals. On an unprepared specimen the lateral line canal is difficult to follow, mainly because the pores are so small and difficult to pick up on the cosmine-coated surface. Surface grinding of the specimen ANU 60029 (Fig. 13C), and observation of other specimens, have exposed the position of the canals clearly. The oral canal runs along the surangular almost parallel to its upper cosmine-covered margin. Towards the anterior end of the labial pit, it curves forwards into the dentary. In its posterior course it is covered by a thin layer of bone, but further forward it sinks into the bone, and under the dentary it is more than 1 mm deep. The canal runs forward on the dentary and as it approaches the forward part of that bone it turns rather abruptly medially, and makes a shallow arc parallel with the anterior edge of the mandible. In this region the boundary of the canal is not sharply defined within the bone.

The mandibular canal enters the angular in its posterolateral corner and runs obliquely across the angular. It produces a transverse commissure on the postsplenial, and the long straight forward branch on the postsplenial is well exposed. This meets the oral canal ventral to the anterior end of the labial pit. The commissure is clear and it has a strong arcuate course towards the midline of the mandible.
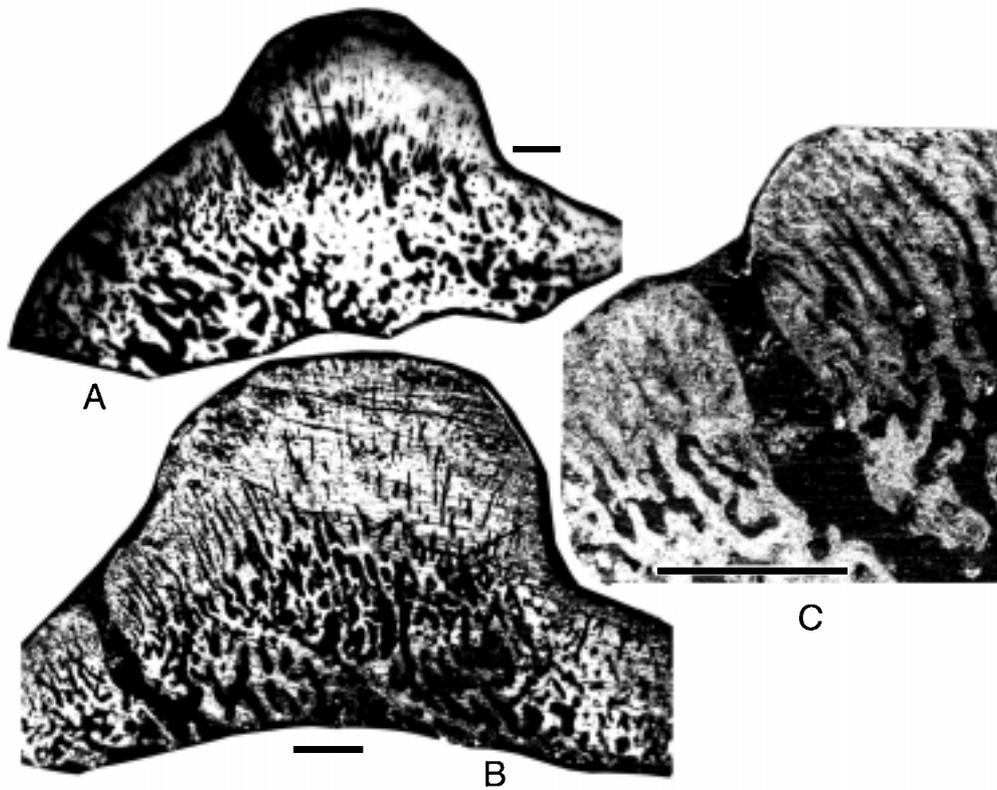
Figure 14. *Dipnorhynchus kurikae*, ANU 60030. Thin sections of the dorsal surface of the anterolateral part of the dentary of the specimen shown on Fig. 11. A—image of a section across the ridge on the dentary, produced by a direct photographic print of the section. The anterior edge is to the left, and the pores in the outer surface are the large depressions in the dentary. B—SEM section from the surface adjacent to A. Anterior edge to the left. The ridge is made of material with long canals which extend up from the dentary, the canals dividing towards the external surface, though this is difficult to see on the photograph because the specimen has been split by structural cleavage. The tissue of the dentary is largely vesicular, but it turns into more tubular canals towards the outer surface. C—left side of Fig. 14B, showing some detail of the microstructure, the detailed similarity between the tissue of the outgrowth and the dentary. Scales = 1.0 mm.

As would be expected because of the elongate middle section of the mandible, the posterior commissure is situated well forward of its normal position on later genera. It is 15 mm from the posterior edge in a mandible 50 mm in median length.

Comparison should be made with the canals on *Dipterus valenciennesi* (Jarvik, 1967: fig. 6) and *Chirodipterus australis* (Miles, 1977: fig. 102), both of which retain the primitive condition of four infradentaries. Nevertheless they have short surangulars, expanded angulars, and lateral line canals which almost run together in the angular. This is a derived pattern developed from the structures we have described for *D. sussmilchi* and *D. kurikae*.

Glenoid region of the mandible. The articular is well exposed on the original specimen described in 1985, and it is even more complete in ANU 60028 (Figs. 9A, 10A,B, 12A). The glenoid is a large structure which opens posterodorsally, and it has a slight flexure laterally, indicating a weak double joint. This is not nearly so pronounced as the lateral joint in *Chirodipterus australis* (Miles, 1977: fig. 104). Because it is open posteriorly the design of the joint does not provide a stable pattern for opening and closing the mandible, especially if large food items had to be processed. Two other features stabilise the joint. A posteromedial process has a dorsally projecting structure on the prearticular which is usually named the pterygoid-mandibular ligament process. It is often partly destroyed by wear, or it has a more flattened structure, but on ANU 60028 it is an elevated structure with a ligament attachment surface on its posterior face, and a separated scar on the anterior face (Fig. 10A,D). It may be that this process is unusually well developed on this one specimen, but it is so exposed that it could easily have been destroyed by wear on the other few specimens. This process is situated at the rear end of the glenoid, but would not be well situated to prevent posterior dislocation of the articulation.

The preglenoid process has a high rough surface on the articular standing 5 mm above the denticulated edge of the surangular (Fig. 10A–D). To this surface was attached a ligament or a muscle from the adductor chamber in the upper jaw. It is much stronger than the pterygoid-mandibular ligament, and probably was the main stabilising feature for the articulation. It is certainly in a position to help to arrest the posterior dislocation of the articulation. A similar, but smaller, process is present on other specimens of *Dipnorhynchus*, and on *Chirodipterus australis*, which also has an open posterior edge on the glenoid.

Adsymphysial region. We have four specimens of mandibles with the adsymphysial region preserved. Two of them have the anterior furrow divided by the prearticulars joining with the dentary and two do not (Figs. 9A, 10A, 11A, 12A, 13A). Examination of the former shows that the whole prearticular is extended forwards at depth, and the dentary is bent backwards to make the join which is solid bone. There is no indication that the connection is the result of a dental-plate making the join across a gap in the bone, unlike *Chirodipterus* which has an isolated bone lying across the anterior furrow nor *Holodipterus* which has a large plate wedged between the dentary and the prearticulars, but with a free base (Pridmore *et al*., 1994). Nor is there any evidence that the anterior edge of the prearticulars in *D. kurikae* has sutures that could be interpreted as boundaries of an adsymphysial plate. Thomson & Campbell (1971: fig. 20) illustrated a structure labelled coronoids in this position, but its outline was indefinite and subsequent discoveries have convinced us that no separate bone exists in that position.

Clearly the presence of such a plate is not definitive of the Dipnoi, as it is absent in the primitive dipnorhynchids. Its origin remains a puzzle as although it is present in chirodipterids and holodipterids, it does not seem to be present in dipterids nor in rhinodipterids. It may be that it occurs as a neomorphic structure in several dipnoan stocks. So far as we can determine, no similar structure occurs in *Diabolepis*.

Prearticulars. These bones are very similar to those of *D. sussmilchi*, but the large tuberosities behind the anterior fossa are not connected back to the posterior tuberosities, and the transverse gap between the two is wide and shallow. Similarities that need to be emphasized are the patch of denticles at the corner inside the articular contact (Figs. 9A, 10A), the mass of denticles in the lingual furrow (Fig. 10A) and the posterior edge of the large posterior tuberosities. These leave a sharp edge on the tissue around the margins of the dental plate, indicating the backward growth of the plate.

The posterior tuberosities are not all of the same shape, some having the appearance of high rounded surface (Fig. 9A,B) and others being somewhat worn down. The high ones have one or two rounded furrows around them, the inner mounds being higher than the outer ones. This gives the appearance that the tubercles grew periodically during the growth of the animal. This would be a unique way for the dental plate to grow in a dipnoan, and it will be discussed below.

Growth of dental plates

We have to explain the growth of both upper and lower dental plates, as they are obviously complimentary structures. The dental plates of the mandible will be discussed first, and those of the palate will be discussed secondarily as we have less well preserved material available for sectioning.

Growth of the prearticular dental plates. White (1966) figured a prearticular tooth plate of *D. sussmilchi*, and commented that the blisters (tuberosities) were formed of a thickened layer of dentine continuous with the supporting bone. Denison (1974) did not place *D. sussmilchi* as part of his group with dental plates. He also indicated that its dental plates were covered with dentine, and commented that there is no evidence of how this dentine formed, or whether it continued to grow next to the spongy bone at its base as the buccal surface became worn. There are two main problems with these statements. Both authors accepted that the tissue forming the surface of the dental plate was dentine, although they could not understand how it formed; and secondly they assumed that the worn surface of the plates would remain worn because dentine could not be added to the surface once the original dentine had been deposited. These problems have been continued by subsequent workers who have assumed that dentine was present, though some workers have noted that the surfaces of the tuberosities were modified by later growth (Campbell & Barwick, 1985).

Not only has it been a problem with dipnorhynchids, but it has carried over into the understanding of *Speonesydrion* in which a bulbous mass of tissue forms the heel of the plates in the mandible (Campbell & Barwick, 1984; Smith, 1986). The more lateral parts of the plates in *Speonesydrion* have enamel covered teeth which have the usual dipnoan characteristics, even though the oldest parts of hard tissue lying on bone, and were modified by growth as in dipnorhynchids.

In *D. kurikae*, the left and right plates continue across the mid-line of the mandible without a break, and no mid-line suture is present. Consequently the dental plates cannot be added to by median growth along a suture, as is normal for dipterids, chirodipterids and later genera. We consider the dipnorhynchid pattern to be a primitive feature of dipnoans, and the development of the median suture appeared in the later Emsian probably in such genera as *Tarachomylax* Barwick *et al*., 1997, and it became the means by which dental plates evolved by addition at the mid-line. Secondly the occlusal surfaces of the tuberosities are in some specimens rounded, as is shown by Figs. 1A, 9A,B and show no signs of wear. This occurs in both the large posterior tuberosities and the smaller anterior ones. The surfaces of some tuberosities are not smooth, but show grooves which are subconcentric or irregular in their distribution (Fig. 9B). In the mandible the central part of the tuberosities is highest and well rounded indicating that it was the most recently added sector. Obviously the tubercular part of the plate did not increase in size laterally as they did later dipnoans, nor did they modify their shape in the oral cavity by growth at the plate margins. Yet they did increase in size during growth of the animal, as did the marginal ridges.

A thin section of the large posterior tuberosity on the mandible is illustrated in Fig. 15. It also shows the thick bony layers of the tuberosity in which the growth took place at different rates and produced the shapes shown externally in Fig. 9B. It also shows the thin layer of surface tissue (dentine) in which the canals are vertical to the tooth-plate surface. In particular, we illustrate the surface between the tuberosity and the marginal ridge in which the surface layer is well preserved (Fig. 15A–C). It was by the resorption of this layer, or by the addition of new canals between the original ones, which allowed the shape of this part of the plate to change during growth. Detail of this layer is shown on Fig. 16A, in which the vertical columns of dentine are still visible though some post-mortem changes have taken place. The marginal ridge is not well preserved in the thin
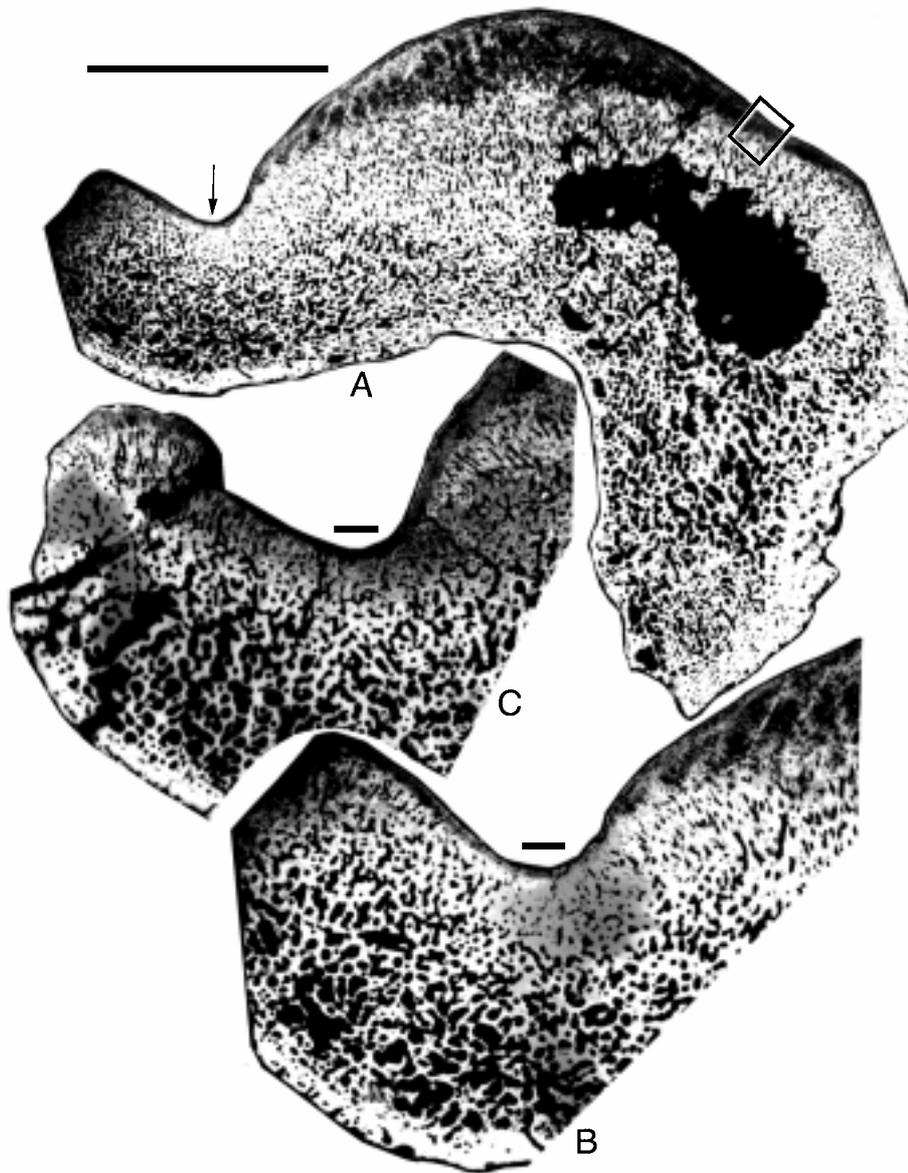
Figure 15. *Dipnorhynchus kurikae*, sections across the posterior tuberosity of ANU 35643. A—an almost complete section, lateral ridge (slightly incomplete) to the left and the lingual surface to the right. The dark coloured material on the dorsal surface is the tissue was added to at its junction with the adjacent bone during the growth of the plate. The gap in the centre is the result of loss during grinding. Compare with White (1966: pl. 1, fig. 1). B—enlargement of the lateral ridge and adjacent surface. Note the thin dark layer on the surface, the underlying tissue with elongate columns, and the thinning out of the surface tissue in the groove. Note the thin layer of fine texture on the surface on the left side. C—section cut adjacent to A and B, but with the marginal ridge well preserved, though broken across. Note the elongate tubes forming the bulk of the marginal ridge and the way it dies out laterally against the prearticular. Scales: A = 10 mm; B–C = 1.0 mm.

sections, but the canal-like tissue thickens into the ridge on its medial side but laterally it thins out onto the prearticular. An enlargement of the outer surface of the posterior tuberosity outlined on Fig. 15A, is given in Fig. 16B. This shows the columns of tissue growing upwards from the prearticular. On the outside surface of the bone is a very thin layer of harder tissue, only 0.3 mm thick. This thin layer also occurs on the tubercle although it is not so well shown on the photograph. The continuity of this layer across the whole dental surface indicates that it was formed from a layer of surface tissue which originally covered the dental surface, or by modification of the ends of the bony columns underlying it. The first suggestion requires the covering of the dental surface at sites which are active in biting, and scarcely seems a possibility. We prefer the second view, but do not have an explanation of the process involved. The section also shows some thin horizontal tubes which are the result of post-mortem effects.

The arrangement of the bony tubules in the space between the tuberosity and the marginal ridge, must have been the result of resorption of bone and the deposition of new bone at specific locations. As indicated above, this is well illustrated by Figs. 15, 16 and 17, which also follow the pattern illustrated by the overgrowth on the dentary as in Figs. 14A–C (see discussion below). This process may cause difficulty in interpretation of the growth process but, given our observations, we can see no alternative.

The lateral and posterior margins of the prearticular plates show no increase in the wear surface of the tooth plate except for the small denticles around the edge of the plate. These denticles are overgrown by extension of the continuous tooth plate tissue over the tubercles. This allows the marginal ridge to be modified in shape, and the form of the lingual cavity in the mandible to be modified with further growth.

All the above points indicate that:

1. plate growth did not take place by the addition of marginal growth in the form of teeth as in other dipnoans;

2. plate growth did not take place by the addition of new layers of tissue at the mid-line, nor did resorption of the plate take place at the mid-line of the palate or the mandible;

3. there are no homologues of real teeth in the system;

4. the marginal ridges were added to by resorption at their inner edges, and the deposition of new bone to expand the ridges and the inner face of the palate or the prearticulars;

5. lateral growth of the plates in both jaws took place by the overgrowth of the small denticles around the plate margins, and posterior growth by similar overgrowth on tubercles in the labial cavity;

6. vertical growth of the plates in both jaws must have taken place by the upward growth of the tuberosities and the surface tissue between them by differential bone growth from within the plate tissue, and addition to the base of the dentine layer;

7. this whole pattern of growth is completely different from any other dipnoan, and in our view represents a first step towards development of palatal biting by dipnoans, one of the most distinctive features of the group.

The understanding of this type of growth is provided by the outgrowth on the dentary which is so well shown on ANU 60029 and ANU 60030, and illustrated on Fig. 14. To check these points it is necessary to prepare thin sections of the material to examine the structure of the tissue.

Thin sections of the ridge on the dentary of ANU 60030 show some geological structural cleavage, but the biological structure remains clear. The bone of the dentary is vesicular. It passes over a roughly defined boundary into vertically organised tissue through which long tubes extend to the external surface. Although many canals are continuous, others are branched. Towards the edge of the ridge the canals bend towards the margin of the ridge, and merge with the pattern of the canals in the dentary. The hard tissue must have been laid down around the individual tubes, the tissue around adjacent tubes meeting at a dark line in vertical section. The internal structure of the hard tissue is homogeneous. No dentine tubules are present within the tissue.

The deposition of this ridge tissue is a matter of major concern. No sign of the original surface of the dentary under the ridge is preserved. It must have been resorbed and new coarse vesicular bone tissue was deposited extending up
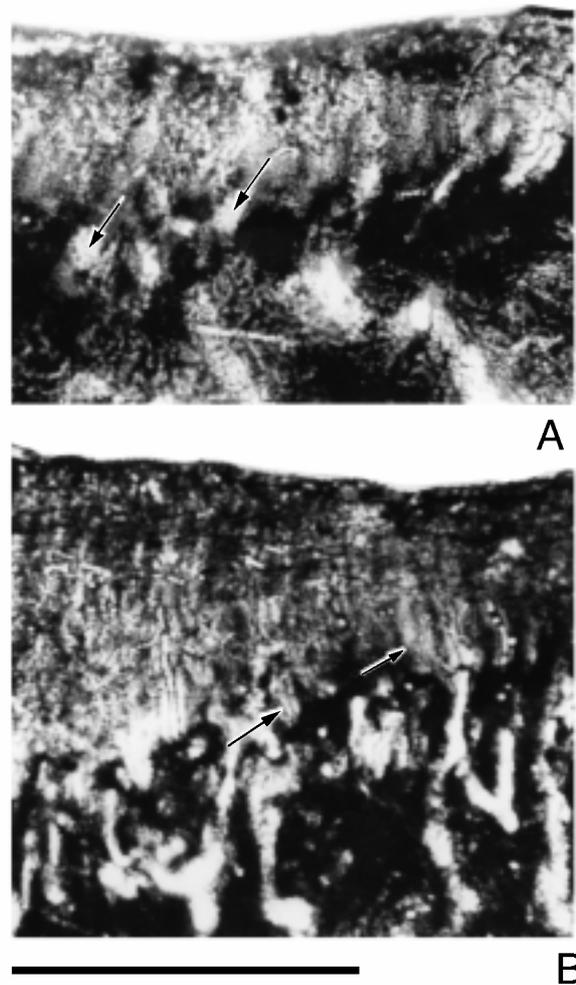

Figure 16. *Dipnorhynchus kurikae*, thin sections of ANU 35643 photographed to show detail. The specimen was slightly altered during preservation, and some of the detail has been lost. A—surface tissue in the valley between the posterior tuberosity and the lateral ridge, indicated by an arrow in Fig. 15A. The external layer shows traces of columns of bones (arrowed) lying on coarsely vesicular prearticular. B—section of the posterior tuberosity as marked on Fig. 15A. This shows more clearly the structure (arrowed) of the surface tissue. Vesicular tissue in the lower parts of the sections. Scale = 1 mm.

into the base of the ridge during growth. The ridge itself contains elongate tubes which reach to the surface, and this would have been deposited by mineralisation transmitted through the older bone beneath. In summary then, the depositional process involves the modification of the older bone, its replacement by new vesicular bone and the growth of new vertically arranged bone around the outer surface. The fact that the materials are all bone and no dentine is involved, accounts for the absence of a pulp cavity and the lumpy arrangement of the ridge tissue, points which both White (1966) and Denison (1974) were unable to comment upon. This pattern provides the basis for the interpretation of the periodically growing bone-based dental plates.

The mandibular structure of *Diabolepis*, with its prolingual field, a short symphysis, and a median gap which opens easily to allow the two halves of the mandible to be preserved
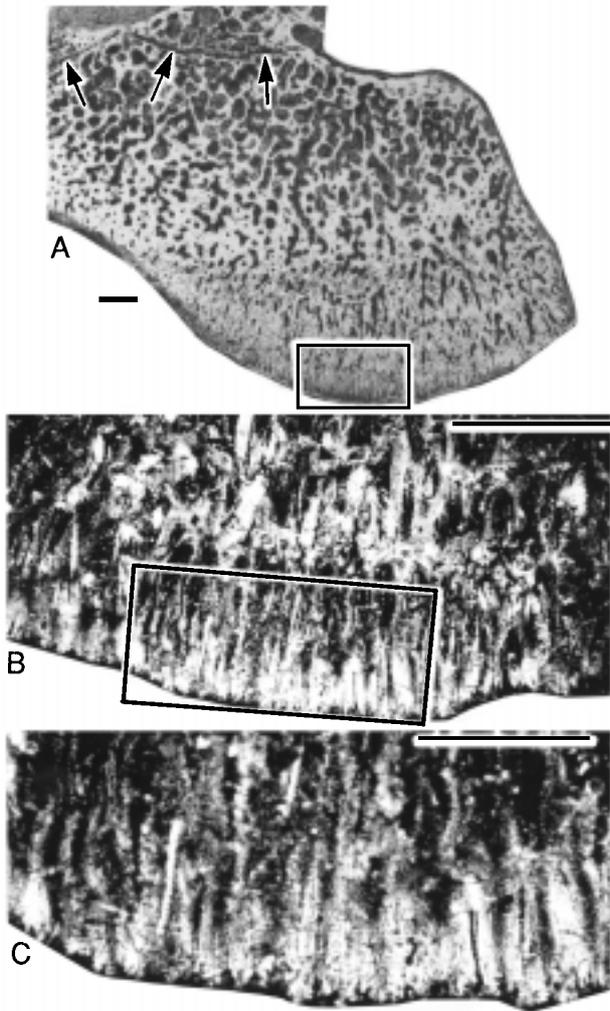
Figure 17. *Dipnorhynchus kurikae*, sections across the anterior palatal tuberosity of ANU 36508, figured by Campbell & Barwick (1985: fig. 6d). A—direct photographic print from the section. The boundary between the pterygoid and the neurocranium is shown by arrows at the top. B and C are printed from negatives made from the palatal face of the above section. B is from the area of the rectangle in Fig. 17A, and shows the tuberosity near the base. The coarse tissue at the top of the photograph corresponds with the coarse tissue between the fine tubular tissue and the coarser tissue against the vesicular bone in Fig. 14A. C—enlargement of the rectangle in Fig. 17B, and shows the tubes towards the biting surface. No dentine tubules are visible. Scales: A = 10 mm; B = 0.5 mm and C = 0.25 mm.

separately (Chang, 1995), has nothing similar in structure to this pattern whether one agrees with its interpretation or not.

Growth of the palatal dental plate. The only palate we have for sectioning is ANU 36508. Its surface has been subjected to wear during preservation, and so the grinding surface has been removed. However, enough tissue is preserved on the anterior tuberosity to prepare a study of the histology. A section across this part of the plate was figured by Campbell & Barwick (1985: fig. 6d). The tuberosity on the right of that figure is also refigured herein (Fig. 17) at larger magnifications to show the detail of the canals. The specimen has a large number of post-

mortem borings through the bone, but the details remain clear. The canals and the hard tissue are almost identical to those described above for the ridge on the dentary. There is no sharp boundary between the pterygoid bone and the tissue making up the surface of the lateral tuberosity. As can be seen from the figures mentioned above, that tissue consists of columns like those on the surface of the prearticulars. This dentine-like substance is without dentine tubules, and is connected with the adjacent bone without any sign of a pulp cavity. This arrangement makes it possible for the bone making the tuberosity to increase in height by addition to the bony base. Such an arrangement will permit the bulbous surfaces on the palate to develop during growth. We do not have a good section through the posterior tuberosity, but the ends of the canals are well exposed on the layer illustrated by Campbell & Barwick (1985, fig. 6b). This demonstrates the point that the same material occurs across the whole palatal surface.

Conclusions

New discoveries of topotypes of *Dipnorhynchus kurikae* have allowed us to describe a braincase which has been exposed by etching. This is the first braincase of an Early Devonian dipnoan described from an exposed internal and external neurocranial walls, and a moderately exposed otic region. Previous descriptions by Thomson & Campbell (1971) and Campbell & Barwick (1982) were based on external structures of the neurocranium. The similarity of the braincase to that of the extant *Neoceratodus* is striking, and the identification of the various nerves is made without difficulty. In particular, the recognition of the lateral line nerve is clear. The pattern of the elements of the braincase were established early in the evolution of the dipnoans, and subsequent changes have only modified the proportions of this basic pattern.

The second major feature of this material concerns the dental plates. These include large tuberosities and marginal ridges, the cores of which are bone and the surfaces carry thin layers of dentine which contain no dentine tubercles. Because of this, the shape of the palatal surface was changed by new growth of bone, making growth layers of different heights on the tooth plate surface. This is a major feature of dipnoan evolution, because *Speonesydrion*, which has real enamel-covered teeth around the anterior and lateral margins of its tooth plates, begins growth with featureless plates lying on bone, and then adds enamel-covered teeth at a later stage of ontogeny (Campbell & Barwick, 1984). *Speonesydrion* has the other characters of a primitive dipnoan, as outlined by Campbell & Barwick (1987). The appearance of tooth-plated dipnoan genera in rocks older than those containing *Dipnorhynchus* has not been established, though some workers wish to have *Diabolepis* as an early dipnoan. We do not accept this, and point out the difficulties involved with that hypothesis in a paper submitted for publication. Recent papers dealing with *Diabolepis* were primarily concerned with the early evolution of sarcopterygians, and were not specifically concerned with dipnoans. The differences of opinion are illustrated by reference to work by Cloutier & Ahlberg (1995, 1996) and by Zhu & Schultze (1997). In our view, *Diabolepis* is more closely related to *Youngolepis* and *Powichthys* than it is to dipnoans.

Thirdly, sections of the upper lip show a pattern of growth in which an outer layer of bone with elongate canals and

contains large foramen which do not connect with the rostral tubules in the ethmoid capsule, a second layer of bone in which the canal structure is more diverse, and a third layer in which the bone structure is vesicular. This is separated off from the endocranium by a distinct gap. This is probably a distinctive primitive feature of dipnoans as it is also found in *D. sussmilchi*, though no sections of that species have been cut (Thomson & Campbell, 1971: fig. 57).

The lip structure of the species is of importance because of the fact that dipnoans use their lips as part of the buccal suction pattern of feeding. The description of the lips of *D. cathlesae* (Campbell & Barwick, 1999) indicates the extent to which the early dipnoans had lip structures which we interpret as capable of producing a strong suctorial capacity, and *D. kurikae* is the next oldest species with which it can be compared. The lip structure of *Diabolepis*, in so far as it is known (Chang, 1995), is totally different in its disposition.

The presence of an anterior furrow in *D. sussmilchi* is shown to be a feature in *D. kurikae, D. cathlesae, Speonesydrion iani* and *Uranolophus*, and it seems to have been an important feature of primitive dipnoans. It contained soft tissues richly innervated from a ventral direction and so must have contained a sensory system of some kind. So far as we can establish, it does not occur in *Diabolepis*, where there is only an interface between the dentary and the prearticulars. No Early Devonian dipnoan in the NSW sequence has any indication of tooth bearing structures labelled as prolingual field in *Diabolepis*. Finally, the vomers and the labial pit in *Diabolepis* are not of the kind found in the Early Devonian dipnoans. We conclude that *Diabolepis* is not related to the genera which gave rise to the Dipnoi, but is a side branch related to *Youngolepis* and *Powichthys*.

References

Bartsch, P., 1993. Development of the snout of the Australian lungfish *Neoceratodus forsteri* (Kreft, 1870), with special reference to cranial nerves. *Acta Zoologica (Stockholm)* 74(1): 15–29.

Barwick, R.E., K.S.W. Campbell & E. Mark-Kurik, 1997. *Tarachomylax*: a new Early Devonian dipnoan from Severnaya Zemlya, and its place in the evolution of the Dipnoi. *Geobios* 30(1): 45–73.

Bemis, W.E., & R.G. Northcutt, 1992. Skin and blood vessels of the snout of the Australian lungfish, *Neoceratodus forsteri*, and their significance for interpreting the cosmine of Devonian lungfishes. *Acta Zoologica (Stockholm)* 73(2): 115–139.

Campbell, K.S.W., & R.E. Barwick, 1982. The neurocranium of the primitive dipnoan *Dipnorhynchus sussmilchi* (Etheridge). *Journal of Vertebrate Paleontology* 2(3): 286–327.

Campbell, K.S.W., & R.E. Barwick, 1983. Early evolution of dipnoan dentitions and a new genus *Speonesydrion*. *Memoirs of the Association of Australasian Palaeontologists* 1: 17–29.

Campbell, K.S.W., & R.E. Barwick, 1984. *Speonesydrion*, an Early Devonian dipnoan with primitive tooth plates. *Palaeo Ichthyologia* 2: 1–48.

Campbell, K.S.W., & R.E. Barwick, 1985. An advanced dipnorhynchid lungfish from the Early Devonian of New South Wales, Australia. *Records of the Australian Museum* 37(5): 301–316.

Campbell, K.S.W., & R.E. Barwick, 1987. Paleozoic lungfishes—a review. *Journal of Morphology Supplement* 1: 93–131.

Campbell, K.S.W., & R.E. Barwick, 1999. A new species of *Dipnorhynchus, D. cathlesae*, from Wee Jasper, New South Wales. *Records of the Australian Museum* 51(2): 123–140.

Chang, Mee-Mann, 1995. *Diabolepis* and its bearing on the relationships between porolepiforms and dipnoans. *Bulletin Muséum national d'Histoire naturelle, Paris* 17 (Section C) (1–4): 235–268.

Cloutier, R., & P.E. Ahlberg, 1995. Sarcopterygian relationships: how far are we from a phylogenetic consensus? *Geobios* 19: 241–268.

Cloutier, R., & P.E. Ahlberg, 1996. Morphology, characters, and the interrelationships of basal sarcopterygians. In *Interrelationships of Fishes*, eds. M.L.J. Stiassny, L. Parenti & G.D. Johnson, pp. 445–479. London: Academic Press.

Denison, R.H., 1974. The structure and evolution of teeth in lungfishes. *Fieldiana (Geology)* 33(3): 31–58.

Etheridge Jr., R., 1906. The cranial buckler of a dipnoan fish, probably *Ganorhynchus*, from the Devonian beds of the Murrumbidgee River, New South Wales. *Records of the Australian Museum* 6(3): 129–132.

Jarvik, E., 1967. On the structure of the lower jaw of dipnoans; with a description of an early dipnoan from Canada, *Melanognathus canadensis* gen. et sp. nov. *Zoological Journal of the Linnean Society* 47: 155–183.

Miles, R.S., 1977. Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *Zoological Journal of the Linnean Society* 61: 1–328.

Northcutt, R.G., 1987. Lungfish characters and their bearing on sarcopterygian phylogeny. *Journal of Morphology Supplement* 1: 277–297.

Pedder, A.E.H., J.H. Jackson & G.M. Philip, 1970. Lower Devonian stratigraphy in the Wee Jasper region of New South Wales. *Journal of Paleontology* 44(2): 195–251.

Pridmore, P.A., K.S.W. Campbell & R.E. Barwick, 1994. Morphology and phylogenetic position of the dipnoans of the Upper Devonian of north western Australia. *Philosophical Transactions of the Royal Society of London, B* 244: 105–164.

Säve-Söderbergh, G., 1952. On the skull of *Chirodipterus wildungensis*, an Upper Devonian dipnoan from Wildungen. *Kunglinga Svenska Ventenskapsakademiens Handlingar* (4)3: 1–29.

Smith, M.M., 1986. The dentition of Palaeozoic lungfishes: a consideration of the significance of teeth, denticles and tooth plates for dipnoan phylogeny. In *Teeth revisited: proceedings of the VII International Symposium on Dental Morphology*, eds. D.E. Russell, J.-P. Santoro & D. Sigogneau-Russell. *Mémoires du Muséum national d'Histoire naturelle, Paris*, Série C, 53: 179–194.

Thomson, K.S., & K.S.W. Campbell, 1971. The structure and relationships of the primitive Devonian lungfish—*Dipnorhynchus sussmilchi* (Etheridge). *Bulletin of the Peabody Museum of Natural History, Yale University* 38: 1–109.

Westoll, T.S., 1989. A new interpretation of the dermal skull roof of the Australian lungfish *Dipnorhynchus*. In *Pathways in Geology. Essays in Honour of Edwin Sherbon Hills*, ed. R.W.L. Maitre, pp. 76–83. Melbourne: Blackwell.

White, E.I., 1966. Presidential address: a little on lung-fishes. *Proceedings of the Linnean Society of London* 177(1): 1–10.

Zhu Min & H.-P. Schultze, 1997. The oldest sarcopterygian fish. *Lethaia* 30: 293–304.