A NEW SPECIES OF THE LUNGFISH *DIPNORHYNCHUS* FROM NEW SOUTH WALES

by K. S. W. CAMPBELL *and* R. E. BARWICK

ABSTRACT. A new broad-headed species of the primitive lungfish *Dipnorhynchus*, *D. kiandrensis*, is described from an isolated skull roof found in the Emsian (Lower Devonian) Lick Hole Limestone at the Ravine, near Kiandra, New South Wales. It is slightly older than the specimens of *D. sussmilchi* previously described. The existence of extra bones, particularly T and 14, in the cheek of this genus is substantiated. Arguments favouring the existence of H between Z and A in primitive dipnoans are presented. The ethmoidal canals are shown to be less complex in *Dipnorhynchus* than in *Chirodipterus*. Fine tubules apparently belonging to the same general system as the ethmoidal canals are found between the dermal roofing bones and the neurocranium over a wide area of the skull.

A SKULL roof of *Dipnorhynchus* from the Lick Hole Limestone in the Ravine, near Kiandra, New South Wales, provides new information on the roofing bone pattern of primitive lungfishes. The specimen was recovered from locality C54 of Flood (1969), which lies well within the range of the conodont *Polygnathus dehiscens* Philip and Jackson. Further north at Taemas and Wee Jasper this species is not known to occur in rocks younger than the Cavan Bluff Limestone (text-fig. 1). Abundant brachiopods occur at the locality, especially *Spinella yassensis ravinia*, *Athyris waratahensis*, *Howittia multiplicata*, and *Uncinulus australis*. In addition to the brachiopods, the limestones contain a variety of molluscs and rugose corals.

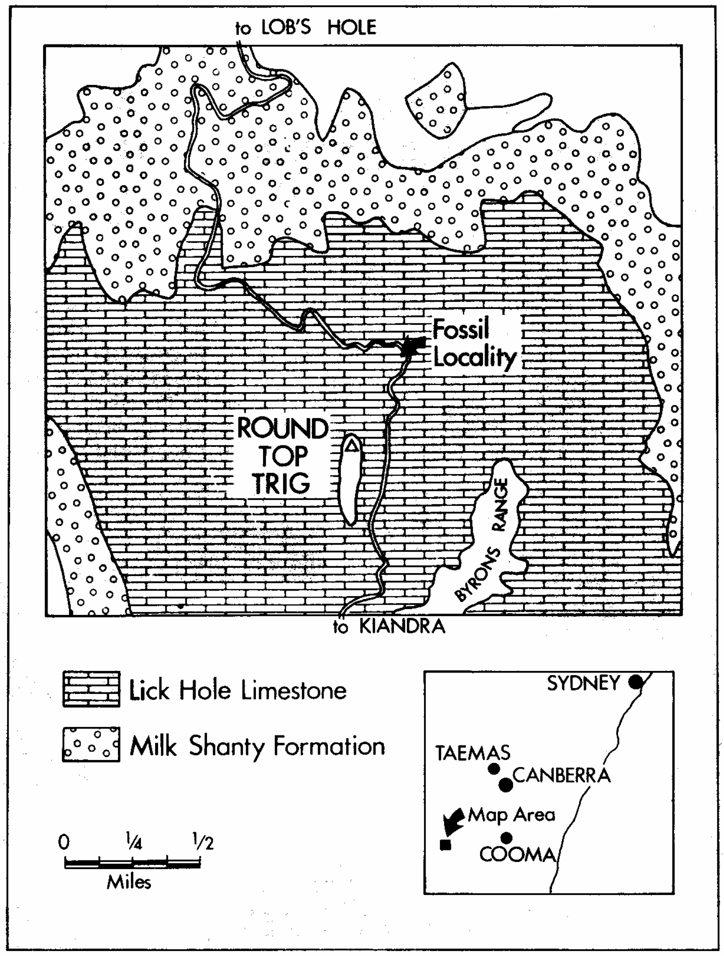
The Lick Hole Limestone is up to four times as thick as the Cavan Bluff, and it has a greater faunal diversity, including some genera, such as the rugose coral *Chalcidophyllum*, found only in rocks above the Cavan Bluff at Taemas and Wee Jasper. It may record a period of time represented by the Cavan Bluff Limestone and at least part of the Majurgong Shale at these localities. A slightly different view is presented by Strusz *et al.* (1972, fig. 2).

Prior to this discovery, the oldest skull roofs of *Dipnorhynchus* were from the *Spinella yassensis* Limestone which, on the basis of either of the above correlations, is a little younger than the Lick Hole Limestone. The new specimen, therefore, is the oldest known representative of the genus in Australia.

Rocks at the locality consist of well-bedded dark-grey limestone interstratified with dark calcareous mudstones. There is no doubt that the environment was marine and the facies is closely comparable with that from which the genus has been obtained previously. No other bone has been found at the locality or along strike from it.

The specimen was found in two isolated pieces of rock on the same outcrop. The pieces fitted together well, but not perfectly, and as a result the reconstruction may be slightly foreshortened along the join. Some of the bones had been removed by weathering, leaving an impression of the bone pattern on the surrounding matrix. By filling the vacated spaces with resin it has been possible to restore these parts of the skull. The right posterior corner of the roof is well preserved so that the outline of Y_2 can be clearly determined, but the median posterior edge is badly eroded, much of I having been removed, leaving no indication of the outline of A. Apart from this, by piecing together information from left or right, or both, it has been possible to reconstruct the roof with the exception of the D bones and those immediately in front of them (see Pl. 52, figs. 1, 2; text-fig. 2).

[Palaeontology, Vol. 25, Part 3, 1982, pp. 509–527, pls. 52–53.]



TEXT-FIG. 1. Locality map, the Ravine, near Kiandra, New South Wales.

EXPLANATION OF PLATE 52

All specimens *D. kiandrensis* sp. nov. (35642 ANU)

Figs. 1-2. Dorsal and ventral views of skull roof.

Fig. 3. Anterior view of snout to show canals of the ethmoid capsule and the anterior part of the lateral-line canals and the ethmoid commissure (arrowed).

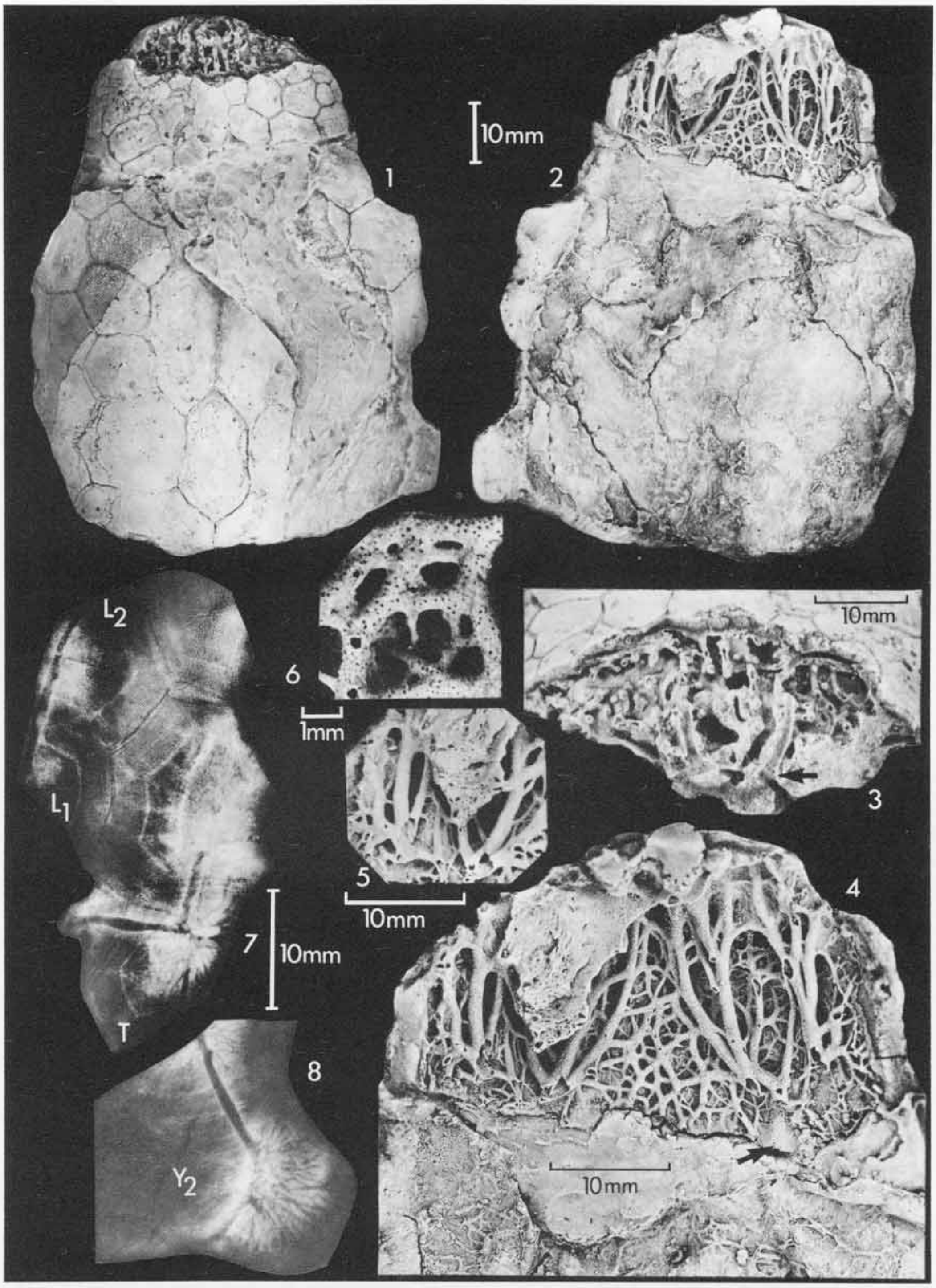
Fig. 4. Enlargement of ventral view of ethmoid capsule. Note the fragment of the roof of the nasal capsule on the left.

Fig. 5. Part of ethmoid capsule with specimen tilted to the left to show the orientation of the canals entering the ethmoid capsule from the nasal capsule.

Fig. 6. Detail from fig. 4 to show structure of the canal bones.

Fig. 7. X-radiographs from right side of skull showing the linkage of the lateral-line canals in bone T and the main canal passing through L_1 and L_2.

Fig. 8. X-radiograph showing the lateral-line canal in Y_2 and part of Y_1 with numerous tubules.


10mm
1
2
L2
6
1mm
10mm
L1
3
5
10mm
4
7
10mm
T
8
Y2
10mm

SYSTEMATIC PALAEONTOLOGY

Infraclass DIPNOI Müller, 1844
Family DIPNORHYNCHIDAE Berg, 1940
Genus DIPNORHYNCHUS Jaekel, 1927
Dipnorhynchus kiandrensis sp. nov.

Etymology. From the village of Kiandra, the nearest settlement to the type locality.

Holotype. 35642 ANU, Geology Department, Australian National University, Canberra.

Horizon and locality. Lick Hole Limestone (Emsian), the Ravine, near Kiandra, New South Wales, Australia.

Differential diagnosis. Skull transverse; most roofing bones more transverse in outline than their homologues in *D. sussmilchi*; interorbital width *c*. 183% of the length of the bones B+C; only two or three lateral line bones between M and the sharp medial flexure of the canal on the snout; bone 14 extending up into the Y_1–Y_2 line; cheek below the Y_2–14–T line probably mobile; operculum lying below the level of the lateral edge of Y_2.

Discussion. This is only the third good skull roof of *Dipnorhynchus* to be found, and consequently little can be said about species variation within the genus. The two skulls of *D. sussmilchi* show considerable differences in the expression of the C bones, the relative sizes of Y_2 and Y_1 and apparently in the number of preorbital bones, and it is difficult to know if this new roof just extends the range of variation in what must be a variable species, or if it is a separate species. Early dipnoans such as *Dipterus valenciennesi* show a wide range of variation patterns in the skull roofs, and species of *Dipnorhynchus* may be expected to show similar ranges.

However, the skull specimens of *D. sussmilchi* come from the *Spinella yassensis* Limestone which is appreciably younger than the Lick Hole Limestone, and the early part of the Devonian is known to be a period of rapid dipnoan evolution. This age difference and the points listed in the diagnosis which show that the new roof can be distinguished morphologically from the two specimens of *D. sussmilchi*, have inclined us to the definition of a new species.

SKULL ROOF

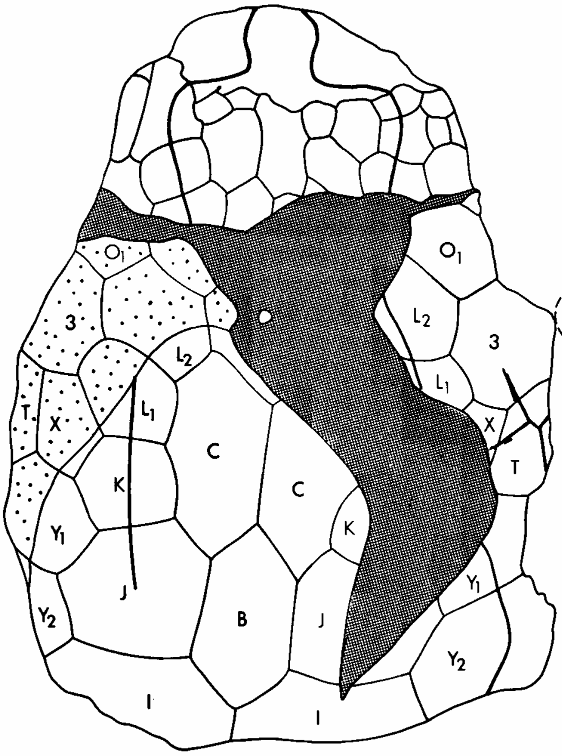
Nomenclature of roof and cheek bones. *Dipnorhynchus* is the oldest dipnoan in which the roof and some of the cheek are known. *Uranolophus*, which is probably a little older, lacks the lateral parts of the roof and cheek. The standard nomenclature for the bones of the dipnoan skull roof and cheek was developed for *Dipterus*. Attempts to apply this nomenclature to *Dipnorhynchus* by Westoll (1949), Lehmann and Westoll (1952), White (1965), and Denison (1968) *inter alia* led to widely differing interpretations. Thomson and Campbell (1971) therefore attempted to list the criteria by which the bones in these primitive forms could be recognized, and showed that the interpretation offered by Denison was the most satisfactory, though he did not include all the bones known at that time. They also showed that there were bones present on the post-orbital part of the skull of *Dipnorhynchus* that were unknown in *Dipterus*, and they inferred the presence of others. These previously unrecognized bones were named and criteria for their identification were listed.

Having done this for the most primitive genera, they proceeded to use what is known of the broad pattern of evolution of the dipnoans, in conjunction with stated criteria for the recognition of fusion or elimination of bones, in an attempt to identify the bones of the roofs of later Palaeozoic genera. In doing this, they were cognizant of the difficulty of using the positions of bones relative to one another as a basis for the identification of bones on the anterior part of the skull, particularly those in the L–N and O–P series. On the other hand, emphasis was placed on the value of canal-canal and canal-pit line junctions in identifying certain bones, particularly X, K, T, and 5; on relations to the neurocranium in identifying others, particularly I, which meets the dorsolateral crista, and D, which is associated with the pineal openings; and on the relation to the palatoquadrate, particularly Y_1 and Y_2.

Since then two important papers on bone nomenclature in the dipnoans have been published by Miles (1977) and Graham-Smith (1978). Miles, basing his conclusions on the theoretical work of Jardine (1969), has strongly criticized the work of Thomson and Campbell (1971), and *inter alia* claimed that the T of *Dipnorhynchus* is a misidentified 4 and that H does not exist. Graham-Smith was also doubtful of the validity of the arguments used for the existence of H. It is not our intention to offer a general discussion of the theoretical issues involved. This we intend to do as part of a later paper on dipnoan evolution. This newly discovered specimen, however, permits us to check previous conclusions on bones T and H, as well as the bones of the posterior part of the cheek. In carrying out these checks we will attempt to show that in discussing the homologues of structures forming complex patterns, it is essential to argue from the most complicated to less complicated situations; that parsimony is a useful guide only in deciding between equally probable hypotheses; that lateral line canals in certain parts of the skulls of primitive forms lie in tubes made of a bony mesh below the dermal bone proper; but that lateral line canal-bone relationships provide the best guides available for the identification of bones on some areas of skull roofs, though they must be used in conjunction with other data.

Roof bones of D. kiandrensis. The roofing bones show a pattern very similar to that of *D. sussmilchi*, the differences being largely ones of proportion (text-fig. 2).

Bone Y_2 is complete on the right side. Its posterior edge is concave in outline, and the bone has a finished margin over most of its width. The shape of the postero-lateral corner shows that the operculum lay entirely below the level of the lateral edge of the bone, unlike the situation in later species in which the operculum truncates the posterolateral corner. This means that the operculum was unusually low in relation to the skull roof.



TEXT-FIG. 2. Diagram of dorsal view of skull roof of *Dipnorhynchus kiandrensis* sp. nov. (35642 ANU). The dark stipple indicates the area of plastic reconstruction and the light stipple the area of impression on the surrounding matrix. × 1·2 approx.

The outline of Y_1 is known from the left side of the specimen, and part of it is preserved on the right. It is a large bone also.

Bone I is incomplete on both sides, but on the right sufficient of it is preserved to permit its outline to be approximately reconstructed from X-radiographs. These show it to be a very transverse bone—proportionately even more so than in *D. sussmilchi.* Although it cannot be proved beyond doubt, the median suture between the I bones is probably proportionately longer than in *D. sussmilchi.*

Bones J, K, L_1, and L_2 are similar to those of *D. sussmilchi* in all respects except their more transverse outlines. Bone X is more equidimensional than it is in *D. sussmilchi.* The result of these different proportions is that the interorbital distance measured between the upper edges of the orbits around the dorsal curvature is 183% the length of bones B+C, whereas in *D. sussmilchi* the corresponding figure is 155%.

Bones B and C are as in the second specimen of *D. sussmilchi,* 18815 ANU—i.e. B is pointed front and back, and the C's are clearly separated. The maximum width of the skull measured around the curvature between the lateral extremities of the Y_2 bones is 219% the length of B+C, whereas in *D. sussmilchi* the corresponding figure is 206%.

The bones D have not been preserved, but the sediment infill of the pineal foramen has been retained on the internal mould. This lies between the anteromedial corners of the L bones as in *D. sussmilchi.* The pineal cavity in the visceral surface of the skull is broad, and a distinct tube occupies part of the right side, without expansion of the termination. There is no evidence of a duct on the left side.

Bone 3 is complete on the right side and shows the characteristic bevelled edge of an orbital marginal bone. Its overall shape is very similar to that of bone 3 in the holotype of *D. sussmilchi* except that it is relatively wider. In front of it, 0_1 is preserved on the right side and most of 0_2 is present on each side. 0_1, at least, is of the *sussmilchi* type.

Although part of the roof is missing along the line of junction of the fragments, and identification of most of the individual bones in the ethmoid region is impossible because of this and the natural complexity of the pattern, it is still possible to make some important observations. The transverse part of the lateral line canal on the snout passes through three bones on the left side, and probably only two on the right, whereas in *D. sussmilchi* (18815 ANU) there are four bones on each side. On any reassembly, the number of lateral line bones between M and the sharp medial bend on the snout can be no more than three, and probably only two; in *D. sussmilchi* there are at least three and on one specimen five. Bone 0_2 is small, and there are two or three small bones carrying the infraorbital lateral line anterolateral to 0_2. These must be 1_1, 1_2, and 1_3. This is similar to the situation in *D. sussmilchi.* In summary, the bones in the snout are definitely fewer in number than in the ANU specimen of *D. sussmilchi,* and probably slightly fewer than in the holotype of that species, though the bones in that specimen are partly obscured by cosmine.

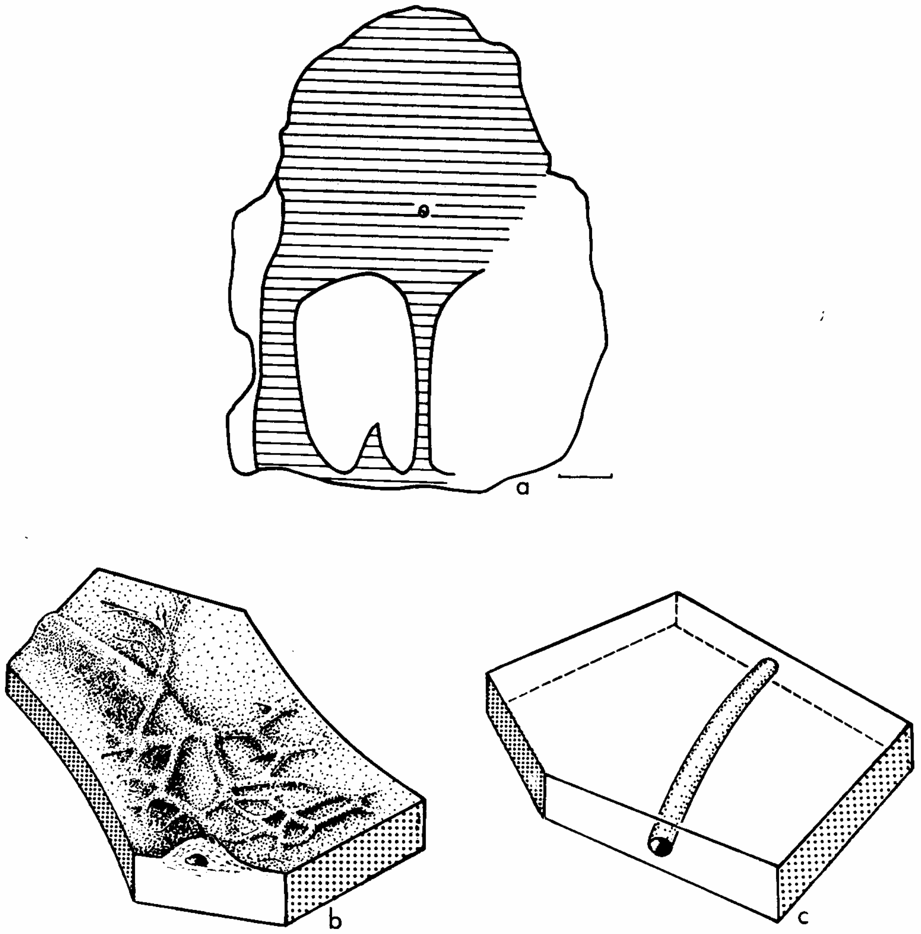
Most of the snout has been eroded, but a tiny part of the upper lip and the paired dermal thickenings on either side of the internasal septum are preserved, permitting a reasonable reconstruction of the snout profile to be made. It does not appear to have been significantly different from that of *D. sussmilchi.*

LATERAL LINE SYSTEM

General. The lateral line canals can be traced by pores, X-rays, and exposed traces on broken surfaces. Over the whole skull the canals are buried deeply in bone, but there are two quite distinct relationships between the canals and the dermal bones determined by the presence or absence of neurocranial bone beneath the dermal bone (text-fig. 3).

On all the specimens of dipnorhynchids and *Chirodipterus australis* we have examined, the form of this junction is similar, and is shown on text-fig. 3. On our new species, where the neurocranium and the roofing bones enclose a space the lateral line canals lie in thickened tubes formed of cancellous bony tissue along the visceral surface of the dermal bones. These thickened tubes are easily visible because they form ridges. They are covered by a continuous thin periosteal layer in the same way as the remainder of the bone surface. Examples are shown on Pl. 52, fig. 4 and Pl. 53, fig. 7, where they are indicated by arrows. Where no neurocranial bone underlies the dermal bone, the canals are buried deeply in the bones, and usually no ridge is visible on the visceral surface of the bones. The same pattern occurs on *D. sussmilchi* and on a specimen of an undescribed dipnorhynchid genus from Cave Island, near Wee Jasper, New South Wales.

The two relationships are thought to be of importance with regard to the possible movement of a canal relative to the ossification centres of the dermal bones during growth. If a canal is buried in a bone, it must pass close to the centre of ossification unless resorption takes place along one wall of the canal and deposition on the other, thus allowing it to move away from the centre during ontogeny. This should show on X-radiographs because the radial bone structure would be disrupted. It is significant that such disruption apparently occurs in bone T where the size and shape of the cross linkage of the canals implies modification during growth. However, X-radiographs show the canal passing through the undisturbed bone centres elsewhere. Furthermore, some resorption must take place to permit the canals to increase in diameter during growth. If the canal lay in a special thickening below the main dermal bone and partly under the influence of the osteoblasts of the neurocranium, it may be easier for the canal to move by resorption and redeposition, and without leaving any distinguishable effect on the radial bone structure. This also opens the possibility for a canal to pass from one bone to another during ontogeny, because peripheral bone growth would no longer be a limiting factor.



TEXT-FIG. 3. *a*, form of junction between dermal bones and neurocranial bone in *Dipnorhynchus kiandrensis* sp. nov. Ventral view of skull roof; crosshatched area indicates dermal/neurocranial bone junctions. *b*, lateral-line canal lying on the ventral surface of a dermal bone. *c*, lateral-line canal penetrating a dermal bone. (Scale = 10 mm.)

In the early stages of dipnoan evolution, the lateral line canals were buried in or below the dermal bone, but by the Late Devonian the canals were usually buried deeply in the bone even though the bones are cosmine covered. In *Chiropdipterus* this is usually the situation, though the canal is exposed on the inner surface as it passes under the neurocranial cover (see Pl. 53, fig. 11) in an occasional specimen. With the loss of the cosmine layer in Carboniferous and later forms, the canals came to lie on the bone surface and then in the skin covering the bones, and so other possibilities of canal movement relative to ossification centres become available.

Lateral Lines of D. kiandrensis. The main lateral line, which lies in a thick tube below Y_2, makes a subangular change in direction near the centre of ossification of that bone. A similar change is noted in *D. sussmilchi*, though it was not shown by Thomson and Campbell. Numerous tubules, many of which bifurcate, spread towards the lateral edge of this bone. In Y_1 the number of tubules is less.

The bone tissue of X, as opposed to its outline, is preserved as a fragment on the right side of the specimen, and the canal can be seen to make a right-angled bend at its centre before passing to T. Canals pass from T to 3, 4, and 14 (see below). These canals do not meet at a point, but rather have a linkage in T as shown on Pl. 52, fig. 7. There are numerous tubules on the lateral half of this bone also.

There is nothing unusual about the supraorbital canal in J, K, L_1, and L_2, but it is better shown on the rostral region than in the specimens of *D. sussmilchi.* The paired canals approach each other closely a short distance above the lip, and join with a short thick commissure. The pore terminating the canal lies in the inner edge of the external naris. As the canal passes over the nasal capsule, the usual thick spongy tube is formed around it.

A fragment of the infraorbital canal is preserved on the right side, passing under the 1 bones where it also is encased in spongy bone. It seems to terminate abruptly well up on the snout, though the surface is not well enough preserved to show the nature of the terminal pore.

The occipital commissure is not preserved, but its inferred character will be discussed below.

The only pit lines on the skull are on I, and they are partially preserved on the left side. There is a long transverse line and apparently a shorter posterolaterally oriented line of the same type as those on *D. sussmilchi.*

BONES OF THE CHEEK

On each side there is a bone behind 3 and lateral to X, the one on the left being incomplete and preserved as a cast, but the one on the right being complete. This is the bone T of Thomson and Campbell (1971). X-rays show that it receives a single canal from X, but three canals issue from it—one to bone 3, a second anteroventrally, and a third posteroventrally. The X-rays also show clearly that the canals do not meet at a point, but rather approach one another, the junction being effected by a cross canal. This bone is clearly not a circumorbital.

EXPLANATION OF PLATE 53

Figs. 1, 2, and 3. Lateral and dorsal views of an almost complete skull of *Chirodipterus australis* (35638 ANU).

Fig. 4. Lateral view of one of the largest specimens of *C. australis* (35636 ANU).

Fig. 5. Skull of an almost complete specimen of *C. australis* (35640 ANU). Note the presence of bones Z and H in the extrascapular series.

Fig. 6. Ventral view of portion of skull roof medial to bones 3 and T in *D. kiandrensis* sp. nov. showing the tubules between the dermals and the neurocranium. Arrows indicate foramina where the tubules emerge through the neurocranial wall.

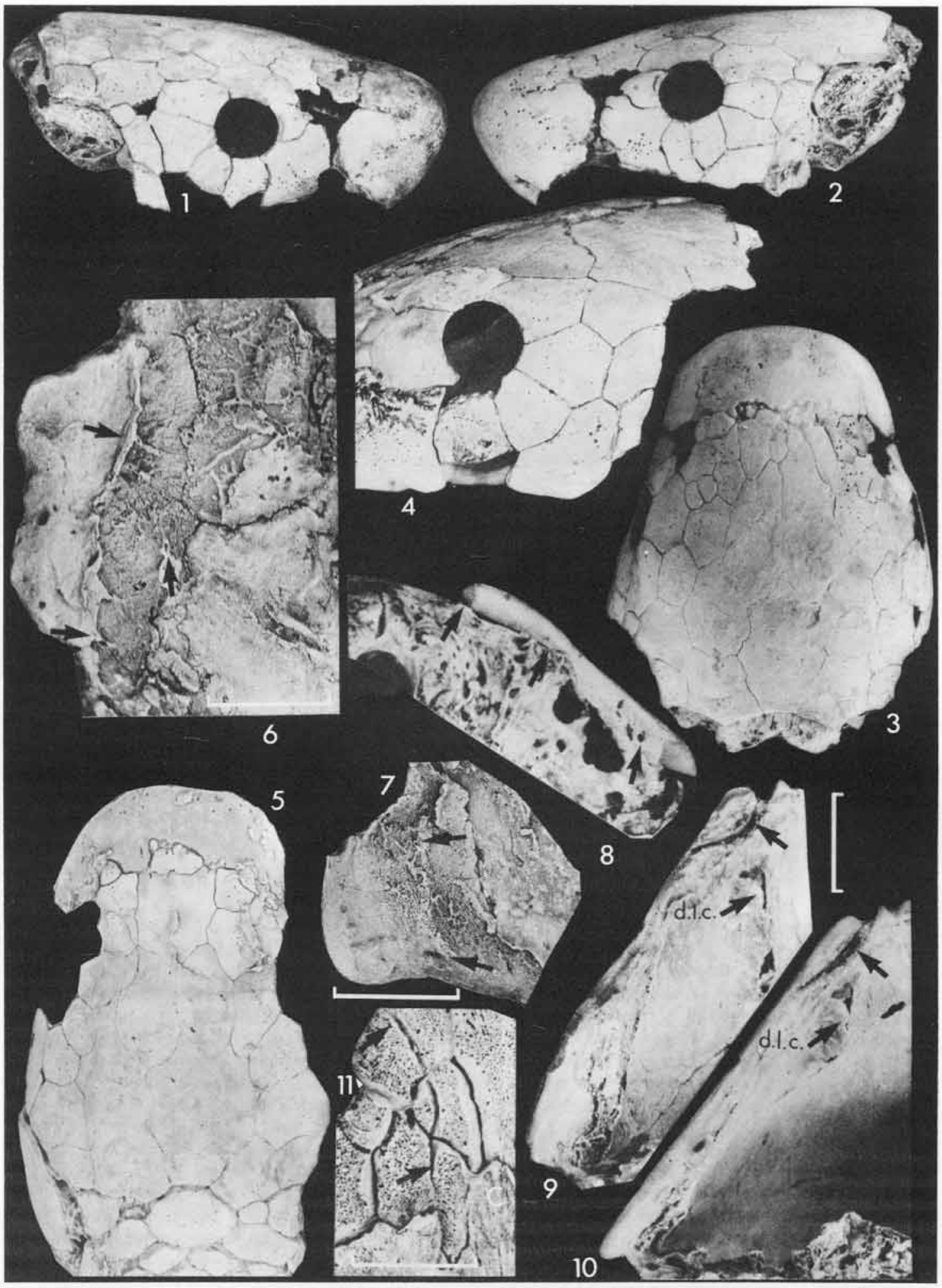
Fig. 7. Ventral view of bone Y_2 of *D. kiandrensis* sp. nov. showing the lateral-line canal lying in a thickened tube overlaid by fine tubules.

Fig. 8. Posteromedial view of the rear of the skull of *Chirodipterus australis* (35639 ANU) showing the open lateral-line canal passing under I and the buried canal Y_2 (both arrowed).

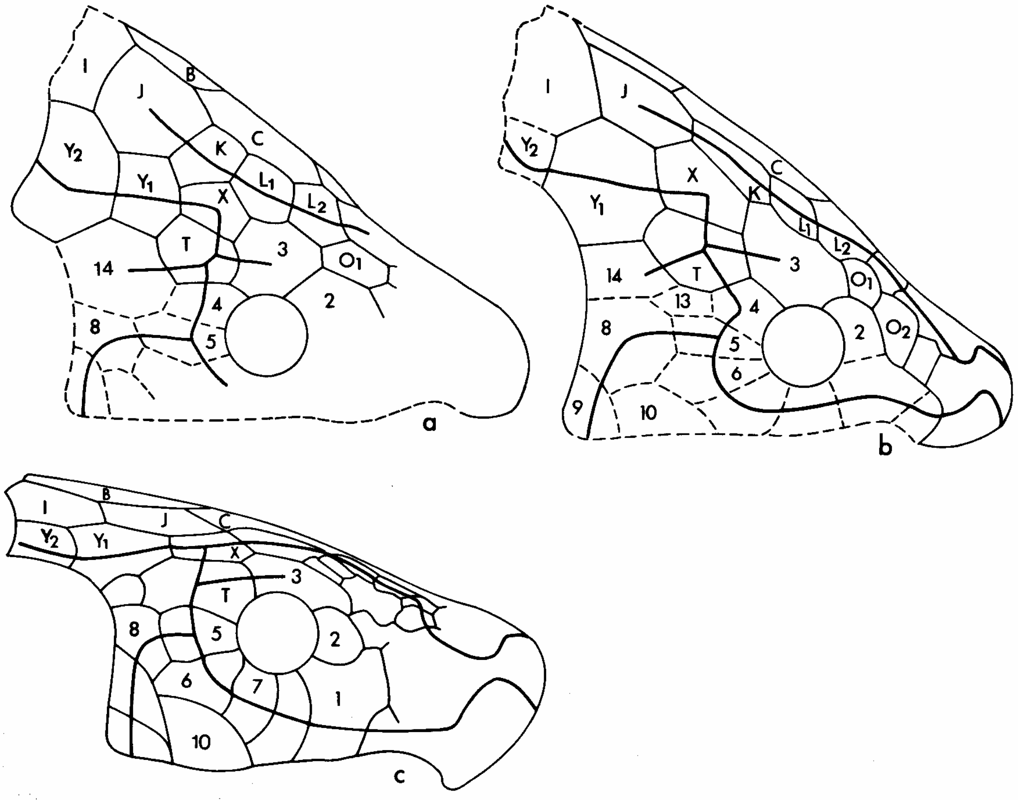
Figs. 9 and 10. Posteromedial and posterior views of the rear edge of the skull of *Dipnorhynchus sussmilchi* (18815 ANU) showing the occipital commissure of the lateral-line canal in I and the tube for the lateral-line canal under Y (both arrowed). d.l.c., dorsolateral crista.

Fig. 11. Ventral view of roofing bones of *Chirodipterus australis* (same specimen as in fig. 4), showing the lateral-line canal emerging from within the bone to lie in an open channel lateral to bone C (arrowed).

The scale bars are all 10 mm long. Figures without scale bars are natural size.



CAMPBELL and BARWICK, Devonian lungfish

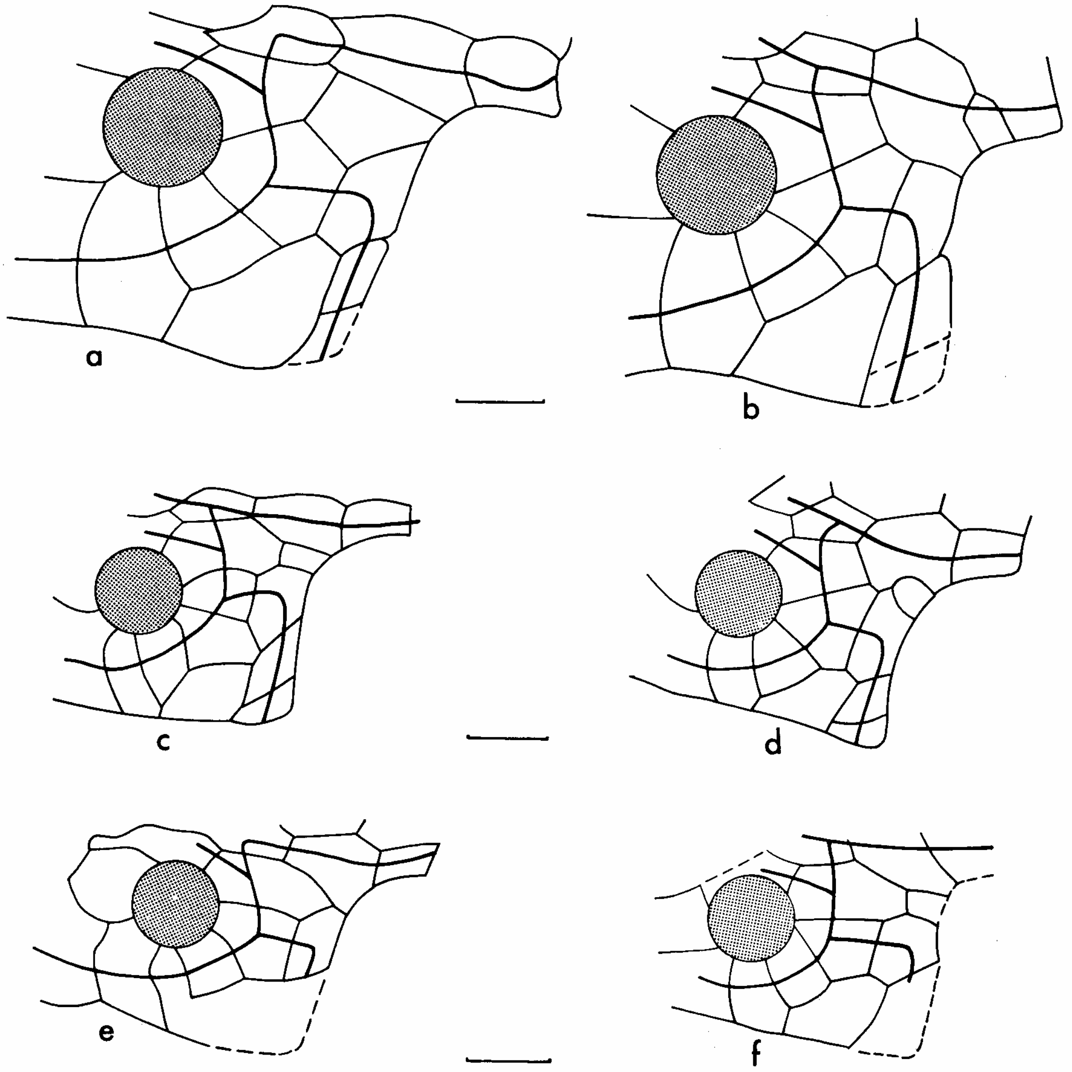


TEXT-FIG. 4. Lateral views of the right sides of the skulls of *a*, *Dipnorhynchus kiandrensis* sp. nov. *b*, *Dipnorhynchus sussmilchi* based on the holotype. *c*, *Chirodipterus australis* based on 35638 ANU. In *a* the lower part of the cheek involves the minimum number of bones possible. In *b*, which is modified from Thomson and Campbell, 1971, fig. 7A, an alternative reconstruction omitting bone 13 and increasing the size of bone 4 is possible.

The anteroventral canal from it must pass into a circumorbital in the *position* of a normal bone 4, and the posteroventral canal must pass into what would have been a large bone (14 of Thomson and Campbell), fitting into a deep embayment between Y_1, Y_2, and T (text-fig. 4*a*). It is clear from the shape of the bone Y_2 that the operculum must have occupied the space beneath it, and that there is no room for a bone 15. The large size of bone 14 is confirmed by the orientation of the lateral line canal passing into it from bone T, leaving little space for a bone 13. Thus, irrespective of the homologies decided upon, it is clear that there were at least three bones (viz. 4, T, and 14) of moderate to large size in *Dipnorhynchus* between the orbit and the operculum filling the space occupied by 4 in *Dipterus*. The pattern and number of these bones varies but, in so far as the evidence goes, bone 14 is higher on the skull and tends to break the Y_2-Y_1 line more in *D. kiandrensis*. This specimen also suggests that the bones of the cheek below the Y_2-14-T line were not fused but capable of movement, the lateral edges of Y_2 and T being clearly bevelled, whereas in the type of *D. sussmilchi* there seem to have been normal sutures in this region.

Discussion. Having established that there are more bones than Miles was prepared to admit, the question of their homologies must now be broached. In particular, it is necessary to examine the claim (Miles 1977, pp. 230, 249) that T is really 4 that has been misidentified. In order to conduct a discussion, it is proposed to use the terminology suggested by Thomson and Campbell for 4, T, and 14, simply so that enough symbols are available. Of course, the symbol 4 must be used for the homologue of 4 in *Dipterus* where it was defined, and it may be that the above usage will prove to be incorrect.

Any interpretation must take account of the disappearance of bone 14, and with it the posteriorly directed canal it contained, for such a canal is not found on any later lungfish. No specimen of *Dipterus* known to us has a bone in the position of 14 (i.e.) below Y, above 8, and bordering the operculum. However, in the ANU Gogo collection of *C. australis* five specimens have nine cheeks sufficiently well preserved to determine the presence or absence of a bone between 4 and the operculum. Of these nine cheeks, three have no extra bones in this position, five have one bone, and one specimen possibly has two (Pl. 53, figs. 1, 2, 4; text-fig. 5). These bones never contain a



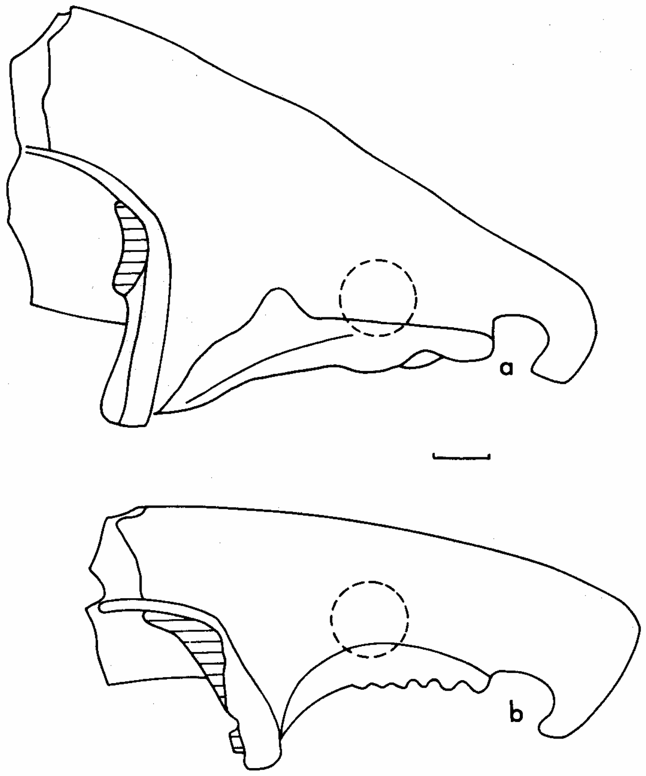
TEXT-FIG. 5. The cheeks of 4 specimens of *Chirodipterus australis* to show variation. *a* and *b*, the cheeks of 35636 ANU, in the same orientation; *c* and *d*, 35638 ANU; *e*, 21639 ANU; *f*, 35637 ANU. (Scale = 10 mm.)

lateral line canal. Because of their sporadic occurrence and the absence of a canal, it may be best to regard bones in these positions as anamestic, rather than 14's (or 15's). This information is intended to demonstrate that in at least one Late Devonian genus with a cheek relatively longer than that of *Dipterus*, there are extra bones forming a pattern like that postulated for *Dipnorhynchus*, and that the cheek figured by Miles (1977, fig. 117) for *C. australis* is atypical in having only bone 4 between the orbit and the operculum. What then has happened to 14 in those genera in which 4 runs the whole length of the cheek? The two possibilities are that it has fused with T or that it has become progressively smaller and has been eliminated.

It is known that bone 8 in *Dipnorhynchus* is large and equidimensional, but as the cheek became shorter in *Dipterus* and *Chirodipterus*, 8 also became shorter, whereas the posterior circumorbitals remained equidimensional or even elongate. Bone 8 cannot be eliminated because there must be a bone behind 5 to carry the lateral line to the lower jaw, though it may take up less space by moving to a posterolateral position on the cheek. The available evidence suggests that the shortening of the cheek was accomplished by the shortening of the posterior bones in the cheek, and therefore one might expect that bone 14 was shortened. Although it carried a lateral line, unlike bone 8 there was no functional reason for retaining it in a short cheek. In addition, it has not been appreciated previously that the height as well as the length of the cheek diminished considerably from *Dipnorhynchus* to *Chirodipterus* and *Dipterus* (text-figs. 4, 6). Although the cheek bones are not known in the first genus, the height of the whole cheek can be estimated from the position of the palate and the quadrates. Some of this height in *Dipnorhynchus* is accounted for by the size of Y_2 and Y_1, but much of it is taken up by T, 13, and 14. Consequently, during evolution there was a tendency for 14 to decrease in height as well as length, and as it was not functionally necessary as a canal carrier, a stage must have been reached where it did not develop, its residual space being occupied by the bone in front.

For the reconstructions of the cheek of *D. sussmilchi* given by Thomson and Campbell there are no bones 4 and 13 available as controls. They were reconstructed to fit the shapes of the spaces whose upper edges were determined by 3 and T (text-fig. 4*b*). In addition, the radiation centre of 4 can be approximately fixed from the orientation of the canal that enters it from T. A similar reconstruction is required by the present specimen. There is no concern about labelling 13, but is 4 correctly identified? Could it not equally well be 5, as it would presumably have to be if the unsupported statement of Miles (1977, p. 230) that T is really 4 is to be accepted? The shape of the loose 8 seen in a specimen from Buchan can be interpreted to mean that this would be impossible, but that interpretation certainly cannot be conclusive. Could the situation be like that in the only known cheek of *Holodipterus gogoensis* (Miles 1977, pp. 238, 248) where 4 is shown as a very large bone withdrawn from the orbit, containing the canal running forward on to 3, and with a process on 3 running around the back of the orbit to meet 5? There are two problems with such a solution. In the first place, none of the three examples of bone 3 that we have from *Dipnorhynchus* show any sign of extending around the posterior margin of the orbit. In the second place, it cannot be assumed that the identification of 4 in *Holodipterus* is correct—that is only one possible solution, and it cannot be accepted by fiat. Would Miles have come to his solution if the more complex pattern of *Dipnorhynchus* had been known before that of *Dipterus*, and its bones used as the basis for the system of nomenclature? This highlights one of the main difficulties in not starting from the most complex known organization when attempting to determine relationships in a reducing bone system (Thomson and Campbell 1971, p. 20). It also shows how an apparently parsimonious approach can lead to the too facile adoption of what seems to be a simple solution to a problem when more complex ones should at least be considered. Parsimony is useful as a means of choosing between equally probable hypotheses, but in its application there is a not uncommon tendency to rule out the more complex solution without adequate consideration of the relative probabilities of two hypotheses. In fact, the concept of equal probability is very difficult to apply in real situations.

As we have seen, irrespective of how they are named, there were bones on the positions labelled 4, 13, and 14 by Thomson and Campbell in *D. sussmilchi*, and that as the cheek became shorter and lower, bone 14 and the canal to it were lost, together with bone 13. Bones T and 4 may have



TEXT-FIG. 6. Lateral view of skulls of *a*, ***Dipnorhynchus sussmilchi*** and *b*, ***Chirodipterus australis*** to show relationships of palate and the lateral wing of the neurocranium to the outline of the skull roof. Hatched area indicates the hyomandibular and hyosuspensory attachment areas. (Scale = 10 mm.)

adjusted in two different ways. In one group, T was retained and moved closer towards the orbit, while 4 was progressively reduced in size. If T did not reach the orbit the posterior part of 3 would expand and may ultimately meet 5. The canal from T to 3 would be retained. In this group are the short-headed *Holodipterus* and *Chirodipterus*, the long-headed *Griphognathus* and possibly *Scaumenacia*. The bone identified as 4 in these genera by Miles (1977) would be T. In a second group of genera, 4 maintained its position and size, ultimately coming into contact with X when T was finally eliminated together with the lateral line to 3. In other words, in this group 4 is the characteristic 4 of *Dipterus*. Along with *Dipterus* in this second group are forms such as *Sagenodus* and *Ctenodus*. We are not suggesting that these groups are monophyletic.

C. australis is of interest in this regard. Miles (1977, p. 230) commented that a canal from 4 to 3 is present in *Holodipterus* and *Griphognathus* and that this 'is surely a primitive dipnoan character'. No mention is made of this canal in *Chirodipterus*. In the ANU collection there are five specimens with bones 3 and 4 preserved, and four of them clearly show a canal passing from 4 to 3. We cannot find it in the fifth. Of the four specimens figured by Miles in which 3 is shown, three have lateral line pits. We conclude that a supraorbital branch from 4 to 3 was normal in *C. australis*, and its apparent absence in two of the nine specimens mentioned above could be the result of a lack of canal definition, or of variation between specimens. His 4 is therefore T.

In summary, we see no reason to accept the unargued and oversimplified statement of Miles that the bone identified by Thomson and Campbell as T in *Dipnorhynchus* is in fact 4, and its corollary that the bone they identified as 4 is in fact 5. There are reasons for believing that a reduction of the cheek bones took place in at least two different ways, and in view of the heterogeneous nature of at least one of the groups of genera defined by these different types of reduction, it seems probable that similar types of reduction took place independently in distantly related taxa.

THE EXTRASCAPULAR SERIES IN DIPNORHYNCHIDS

There has been contention for some time about the normal existence of a bone between Z and A in the extrascapular series of primitive dipnoans. White (1965, p. 26) considered that such a bone was present, and Denison (1968, p. 357) designated it H. Graham-Smith (1978, p. 86) has discussed the matter and has concluded that H probably did not exist in either *Dipnorhynchus* or *Uranolophus*, and Miles (1977, p. 222) makes the odd statement that 'as there is no evidence of such a bone there is no reason to postulate its existence'. On the other hand, Thomson and Campbell (1971) presented evidence that they regarded as indicative of the existence of H in *Dipnorhynchus*. More evidence is now available from *D. kiandrensis* and the new dipnorhynchid genus from Cave Island, referred to above, which has an almost complete posterior edge to the fixed skull roofing bones. The following are the observational data.

(*a*) The space occupied by bone A in *D. sussmilchi* is delineated on 18815 ANU, as shown by Thomson and Campbell. The posterior outlines of the skull of the new dipnorhynchid genus and *Uranolophus* show that A would have occupied a comparable space. Certainly it would not have extended laterally beyond the topographic centre of I.

(*b*) In all three dipnorhynchid specimens and in *Uranolophus*, Y_2 is very transverse in comparison with its homologues in *Dipterus* and later genera. This gives the posterior edges of these skulls an unusually great width, which is emphasized in flattened specimens. Compare, for example, Denison's restorations of the roofs of *Uranolophus* and *Dipterus* (1968, figs. 3*a* and 3*d*). In the primitive genera the width measured from the midline to the extremity of Y_2 around the skull curvature is 41-45% of the total skull length, whereas in *Dipterus* and *Chirodipterus* the figures are 30 and 34% approximately. It is emphasized again that in *Dipnorhynchus*, at least, the skull is not only wide but high. Measured from the level of the palate to the posterior roof crest, the height of the skull in *D. sussmilchi* is *c.* 65% of the skull length as opposed to *c.* 40% in *C. australis* (text-fig. 7).

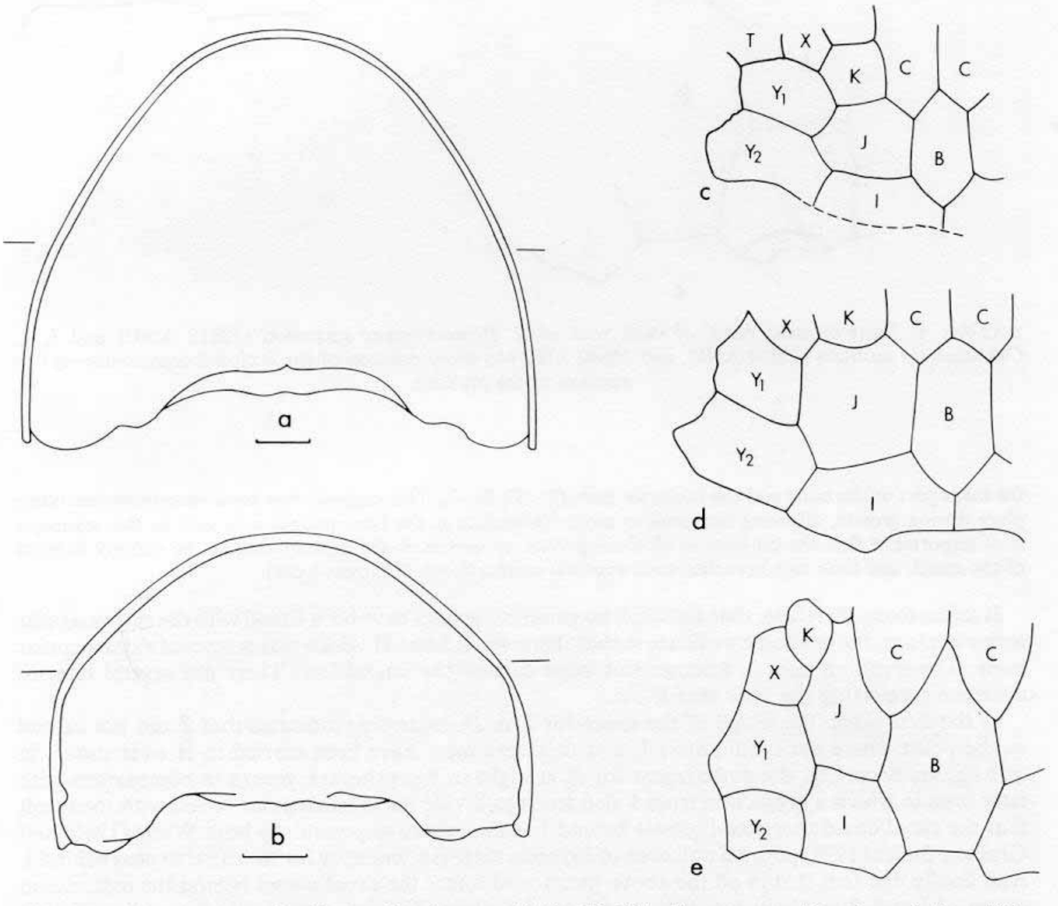
(*c*) The outlines of the posterolateral skull edges on the new genus and *Uranolophus* (Denison, 1968, fig. 3*a*) indicate that Z extended from the edge of Y_2 part way across I, and that a smaller bone lay in an embayment in I between Z and A. Though the edge of I on the *D. kiandrensis* is incomplete, enough of it is preserved to show that the embayment for Z was of the same type. In the ANU specimen of *D. sussmilchi* only the left side is well preserved, and it also shows a similar but weaker embayment.

Of the five new specimens of *C. australis* showing the rear edge of the roof, two are embayed in this position, and one actually shows the bone H between Z and A on one side and a gap in the appropriate place on the other (Pl. 53, fig. 5). This bone does not have the morphology of a scale that extends forwards into the extrascapular series (cf. Miles 1977, p. 222). It is entirely similar to the other extrascapular bones except that it has no lateral line canal. The importance of this is that, despite the fact that though the distance from the outer edge of Z to the outer edge of A is only 22% of the skull length there is a tendency for a bone to develop between Z and A. In *D. sussmilchi* the corresponding figure is 30%, and in *Uranolophus* it is slightly greater.

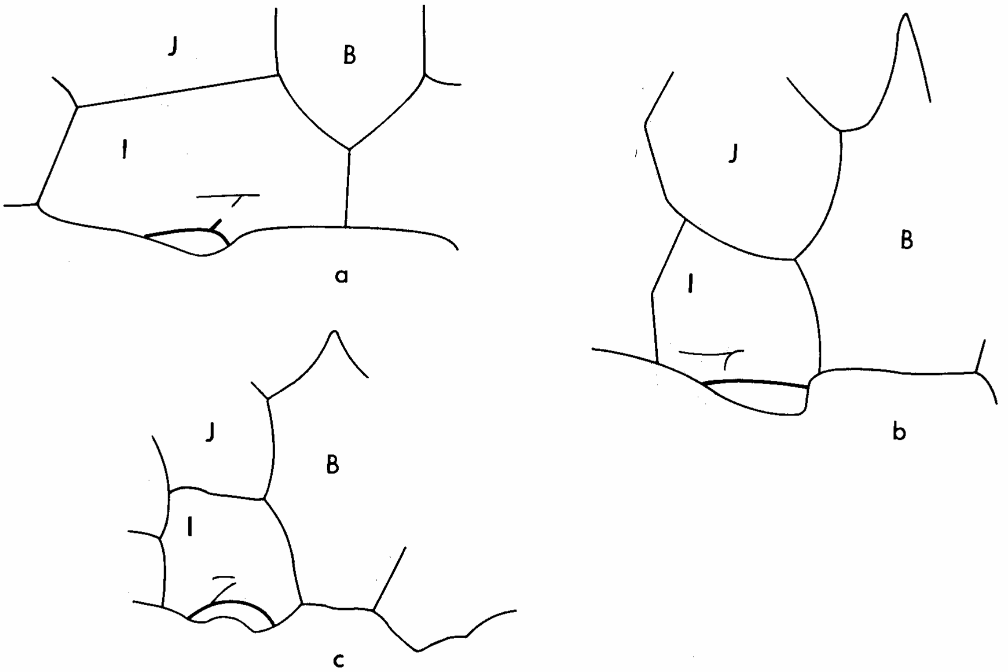
(*d*) We believe that Graham-Smith (1978, p. 86) is in error in stating that 'in *Uranolophus* this part of the skull closely resembles that of *Dipterus*, so that the extrascapular bones, if present, were probably similar'. In the first place, the size of A relative to skull width is much greater in *Dipterus*, as his Figure 21*c* shows. However, his Figure 21*a*, which is based on *Uranolophus* and *Dipnorhynchus*, does not represent either genus in the outline of the posterior edges of Y_2 and I and, assuming that H is not present, the width of Z relative to A is greatly underestimated. He shows A $\simeq$ Z in width, whereas in *Uranolophus* judging from Denison's Figure 3A, A is *c.* 83% of Z, and the corresponding figure for *D. sussmilchi* is *c.* 75%, if there is no H.

(*e*) Further preparation of the ANU specimen of *D. sussmilchi* shows that Thomson and Campbell were in error in concluding that the occipital commissure did not pass through I. In fact it catches the corner of that bone, having a long lateral branch that lies at a high angle to the sagittal line and a shorter median branch turned back sharply to A (Pl. 53, figs. 9–10). At the point of flexure at least one short canal runs towards the ossification centre of I, the main part of the canal passing well behind that centre. The evidence from the new genus from Cave Island is that a canal is present in a similar position, and, although the whole canal has not been directly observed in *Uranolophus*, Denison noted pores on I in two of his specimens and part of a canal in another. It is clear, then, that I was canal-bearing in all three primitive genera known at the present time.

(*f*) In *Dipterus*, *Chirodipterus*, and *Griphognathus* the centre of ossification is displaced well back towards the back of I, and the commissural canal loops forwards towards this centre. So far as we can determine, the canal is embedded in the bone, and does not lie in a spongy tube like the canals under Y_2. The largest specimen of *Chirodipterus* in our collection, however, shows the canal lying in an open slit in the angle between



TEXT-FIG. 7. *a*, Posterior profile of *Dipnorhynchus sussmilchi* and *b*, *Chirodipterus australis* to show relative widths and heights of the skulls. The short horizontal line indicates the lowest extension of Y_2 in each case. *c*, *Dipnorhynchus kiandrensis* sp. nov. *d*, *D. sussmilchi* (18815 ANU), and *e*, *C. australis* (35640 ANU); bones at rear of skulls drawn to same scale and flattened to show relative widths of elements. (Scale = 10 mm.)

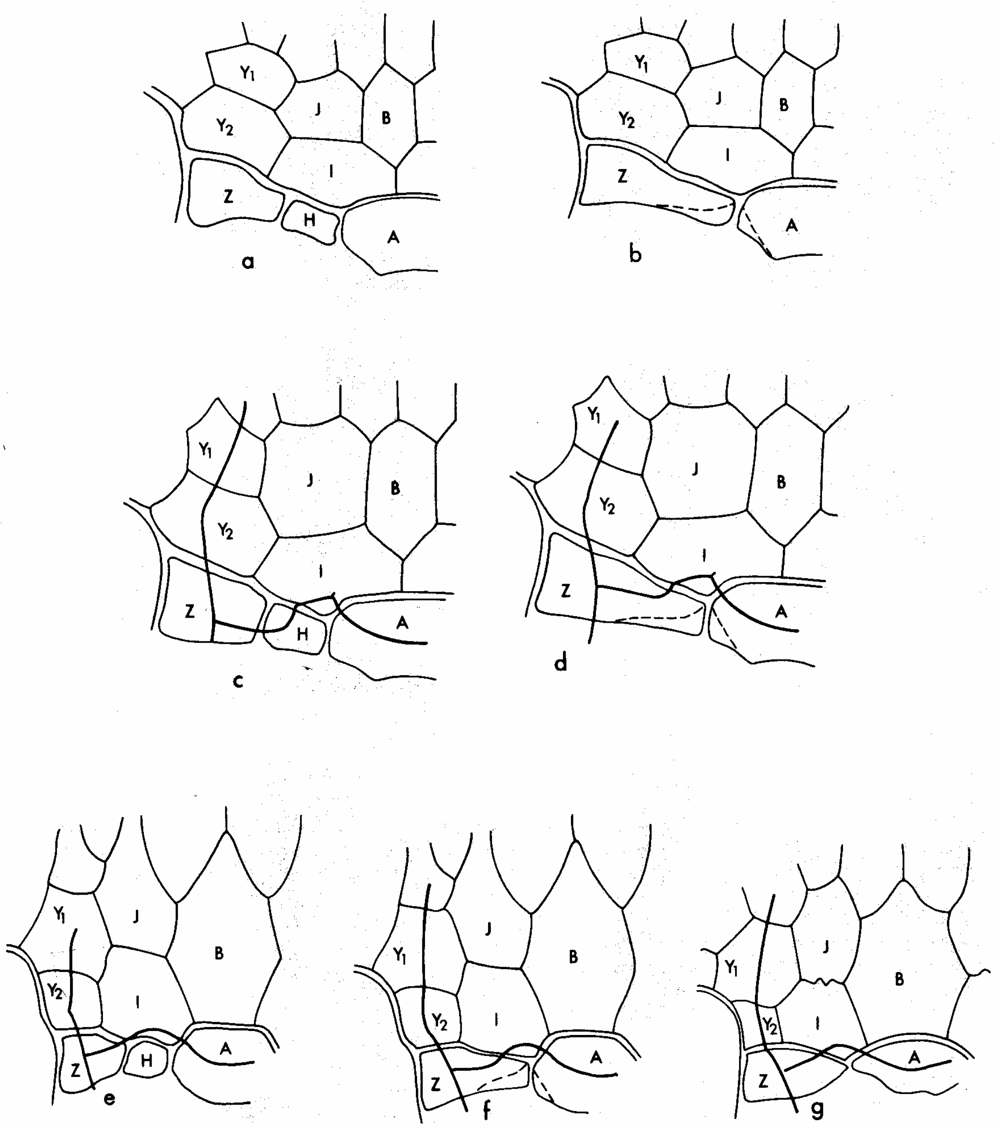


TEXT-FIG. 8. Posteromedial parts of skull roof of *a*, *Dipnorhynchus sussmilchi* (18815 ANU) and *b*, *c*, *Chirodipterus australis* (35639 ANU, and 35640 ANU) to show position of the occipital commissure in I in relation to the pit lines.

the main part of the bone and the posterior horn (Pl. 53, fig. 8). This suggests that some resorption has taken place during growth, allowing the canal to move backwards as the bone increased in size. In this regard, it is of importance that the pit-lines in all these genera, as well as in the dipnorhynchids, lie entirely in front of the canal, and their two branches meet over the ossification centre (text-fig. 8).

It seems to us, therefore, that although no primitive genera have been found with the extrascapular series in place, the available evidence is that there was a bone H which was a normal extrascapular bone. The question now is whether this bone carried the lateral line. There are several lines of evidence supporting the view that it did.

In the first place, the shape of the space for Z in *D. sussmilchi* indicates that Z did not extend to the point where the canal enters I, and therefore must have been carried in H as is shown in text-fig. 9*c*. Secondly, the embayment for A is slight in the primitive genera in comparison with later ones in which a projection from I also tends to divide the extrascapular series, with the result that the canal could more readily pass behind I in the primitive genera. As both White (1965) and Graham-Smith (1978) pointed out, even in *Dipterus* there is a tendency for the canal to pass behind I. And finally, the fact that in all the above-mentioned forms the canal passes behind the ossification centre of I and shows evidence of having moved back in the bone during ontogeny, suggests that it has only moved into I because the bone behind was eliminated (possibly by not only becoming progressively smaller, but also by ossifying progressively later in ontogeny). In this way the neuromasts would become associated with I early in ontogeny (see Graham-Smith, 1978, p. 86).



TEXT-FIG. 9. Left posterior parts of skull roof in *a–b*, ***Dipnorhynchus kiandrensis*** sp. nov.; *c–d*, ***Dipnorhynchus sussmilchi*** (18815 ANU); and *e–g*, ***Chirodipterus australis***, *e–f*, 35640 ANU, *g*, 35638 ANU. The extrascapular series in *a–b* and *c–d* are hypothetical, but the extrascapular bones have been observed in *e* and *g*. The left-hand figure in each set *a*, *c*, and *e* shows the pattern with H present; *b*, *d*, *f*, and *g* show the pattern without H; the dotted lines on Z and A show alternative bone outlines, like those in *g*.

ROOF OF NASAL CAPSULES

The space between the roof of the nasal capsule and the dermal roofing bones (the ethmoid capsule of the tectum nasi) in *D. sussmilchi* is occupied by a mass of ossified rostral canals (Thomson and Campbell 1971, p. 70) whose distribution had to be examined by X-radiography. Similar canals had been noted in *Chirodipterus wildungenesis* by Säve-Söderbergh (1952), and they have been subsequently observed in detail in *C. australis* and *Griphognathus whitei* by Miles (1977).

In *D. kiandrensis* the perichondral lining of the roof of the nasal capsule has been completely removed on the left side and largely removed on the right, exposing the canals. The whole rostral region in this specimen is similar in proportion to that of *D. sussmilchi*. In particular, the ethmoid capsule is depressed in comparison with that of *C. australis*. The maximum height of the capsule in our specimen is 12% of the skull length in *D. sussmilchi* as compared with 17% in *C. australis*, both specimens measured in the median line.

On each side of the midline there are two symmetrically placed major sets of trunks, each of which repeatedly branches. These major canals all lie more or less at the same level, and are not stacked in tiers as they are in *Chirodipterus*. Though it is not certain, it would seem that the two sets of canals penetrated the post-nasal wall through a single foramen and they correspond with the canals for the r. ophthalmicus profundus V and the r. ophthalmicus superficialis VII in *Chirodipterus*. These canals are the ones labelled *prof. m.* and *prof. l.* by Säve-Söderbergh 1952, fig. 4, and by Miles 1977, fig. 66. We have decided on the above homologies because the median set of canals is swinging sharply laterally towards the posterior as though to make a junction, and because the lateral set lies topographically near the suborbital lateral line canal only at its anterior extremity. Only two other nerves enter the tectum nasi of modern genera, viz. the nasalis externus profundus V and the buccalis lateralis VII. Both of these are closely associated with the suborbital canal, and are situated more laterally than the canals in *D. kiandrensis*.

All the canals consist of a delicate meshwork of bony tissue as is shown on Pl. 52, fig. 6.

In *D. kiandrensis* the major canals diminish only slightly in diameter towards the snout where they pass into the thick spongy rind of bone forming the snout. Presumably some of the canals form tubuli that open through sensory pores as is common in other Devonian dipnoans. However, in addition to these there are vast numbers of finer ramifying tubuli whose function is not clear.

The branching pattern of both major series of canals is shown on Pl. 52, fig. 4. There are numerous connecting canals between the major ones on each side, and across the midline. The connecting canals are finer than the major ones. Most of the connections take place via a layer of delicate canals lying close up under the dermal bones. These connections divide and rejoin to form an anastomosis of increasingly finer canals that become appressed to the inner surface of the dermal bones where they either join with their neighbours or pass through the thin smooth layer of periosteum forming the inner dermal bone surface.

A feature that is probably of significance is that a branch of the median series lies almost along the lateral line canal, and small canals from it ramify over the perichondral layer covering the canal. They pierce it, enter the spongy cover, and then presumably join the canal. Certainly where the inner walls of the canal can be observed in the snout region they are perforated by numerous foramina that represent the entry points of the fine canals.

Another set of canals, much fewer in number, penetrate the roof of the nasal capsule and run anterodorsally to meet those in the ethmoid capsule. Some of these are large, particularly those few tucked under the edge of the lip (cf. those labelled *f.m.* and *f.l.* in *C. australis* by Miles 1977, fig. 64). Presumably they represent the paths of nerves that have passed down from the ethmoid capsule into the nasal capsule, and are re-entering the ventral wall of the ethmoid capsule anteriorly.

A final point is that a set of delicate ramifying canals is attached to the visceral surface of the roofing bones in all areas where the neurocranium covers these bones (Pl. 53, fig. 6). These canals are visible in patches on the present specimen, particularly under L_1, L_2, part of 3, T, Y_2, and I. They have a similar relation to these bones as do the fine canals in the ethmoid cavity to their overlying dermal bones, but apparently they exist only in a plane immediately under the surface of these bones. Laterally they penetrate the neurocranial wall under 3 and T, and open into the orbital chamber (Pl. 53, fig. 6, arrows). The specimen of the new dipnorhynchid genus from Cave Island shows these canals better than the Lick Hole individual. In particular, the outlines of the planum antorbitale and the two walls of the median crista against the dermal roof are well shown, and traces of the tubules are observed extending back medially a long distance behind the pineal foramen.

As indicated above we accept the conventional view that the ethmoid canals carried branches of the ramus ophthalmicus profundus V and the ramus ophthalmicus superficialis VII. However, the shape and distribution of the fine canals, especially the fine anastomosing set, outside the regions where they could be involved with the innervation of either a snout sensory organ or the lateral line system, indicates that they permitted the circulation of fluids from the braincase to and from the dermal bones, and/or that they provided the innervation for the sensory organs that are thought to have filled the fine canal system within the cosmine cover of the dermal bones (Thomson 1977).

Acknowledgements. We wish to acknowledge the gifts of the specimen to the Australian National University by the discoverers, Dr. B. D. E. Chatterton and staff and students of Macquarie University, Sydney. Dr. A. Ritchie and Mr. R. Jones of the Australian Museum, Sydney, made the resin preparation from the original specimen. The X-radiographs were prepared by Mr. W. Ambrose of the Department of Prehistory and Anthropology, Research School of Pacific Studies, A.N.U., and printed by Mr. Ivan Fox, Zoology Department, A.N.U. Mrs. L. Wittig and Mr. L. Seeuwen of the Geology Department, A.N.U., prepared the majority of text-figures and the photographs.

REFERENCES

DENISON, R. H. 1968. Early Devonian lungfishes from Wyoming, Utah and Idaho. *Fieldiana* (*Geol.*) **17** (4), 353-413.

FLOOD, P. G. 1969. Lower Devonian Conodonts from the Lick Hole Limestone, Southern New South Wales. *J. Proc. R. Soc. N.S.W.* **102,** 5-9.

GRAHAM-SMITH, W. 1978. On the lateral lines and dermal bones in the parietal region of some crossopterygian and dipnoan fishes. *Phil. Trans. R. Soc. Lond.* (*B*), **282** (986), 41-105.

JARDINE, N. 1969. The observational and theoretical components of homology: a study based on the morphology of the dermal skull-roofs of rhipidistian fishes. *Biol. J. Linn. Soc.* **1,** 326-361.

LEHMANN, W. M. and WESTOLL, T. S. 1952. A primitive dipnoan fish from the Lower Devonian of Germany. *Proc. R. Soc. Lond.* (*B*) **140,** 403-421.

MILES, R. S. 1977. Dipnoan (lungfish) skull and the relationships of the group: a study based on new species from the Devonian of Australia. *Zool. J. Linn. Soc.* **61,** 1-328.

SÄVE-SÖDERBERGH, G. 1952. On the skull of *Chirodipterus wildungensis*, an Upper Devonian dipnoan from Wildungen. *K. svensk. Vetensk. Hand.* **3** (4), 1-29.

STRUSZ, D. L. *et al.* 1972. Correlation of the Lower Devonian rocks of Australia. *J. geol. Soc. Aust.* **18,** 427-455.

THOMSON, K. S. 1977. On the individual history of cosmine and a possible electroreceptive function of the pore-canal system in fossil fishes, *in* ANDREWS, S. M., MILES, R. S. and WALKER, A. D. (eds.). *Problems in vertebrate evolution*, 247-269. Academic Press, London.

—— and CAMPBELL, K. S. W. 1971. The Structure and Relationships of the Primitive Devonian Lungfish—*Dipnorhynchus sussmilchi* (Etheridge). *Bull. Peabody Mus. nat. Hist.* **38,** 1-109.

WESTOLL, T. S. 1949. On the Evolution of the Dipnoi. *In* JEPSON, G. L., SIMPSON, G. G. and MAYR, E. (eds.). *Genetics, paleontology and evolution*, 121-184. Princeton University Press.

WHITE, E. I. 1965. The head of *Dipterus valenciennesi* Sedgwick and Murchison. *Bull. Br. Mus. nat. Hist.* (*Geol.*) **11,** 1-45.

K. S. W. CAMPBELL
Department of Geology

R. E. BARWICK
Department of Zoology
Australian National University
Canberra, A.C.T.

Original typescript received 14 April 1981
Revised typescript received 21 July 1981