A NEW INTERPRETATION OF *AUSTROPELOR*, A SUPPOSED JURASSIC LABYRINTHODONT AMPHIBIAN FROM QUEENSLAND

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Austropelor wadleyi has been something of an enigma to palaeontologists ever since it was named by Longman in 1941. This species, based upon a single fragment of bone found in the Marburg Sandstone of Queensland, was described as a portion of the skull of a labyrinthodont amphibian of Jurassic age. These determinations by Longman of its taxonomic relationships and geologic age would seem to be mutually incompatible, for the reason that all evidence elsewhere in the world indicates the labyrinthodonts to have become extinct at the close of Triassic time. Therefore, if *Austropelor wadleyi* is a Jurassic labyrinthodont, the fossil is of extraordinary significance as being the only record of the persistence of this group of tetrapods beyond the upper limits of the Triassic.

Is the fossil sufficiently complete and of such preservation as to allow its unequivocal identification as a labyrinthodont? Are the sediments in which it was found definitely of Jurassic age?

Romer, in 1947, expressed doubts on both scores. "Neither the nature of the specimen nor the age of the formation appear to be too well established" (Romer, 1947, p. 344). Whitehouse, in 1955, indicated that the specimen could be accepted as a labyrinthodont, for which reason he regarded the Marburg Sandstone as of Triassic age. "Recently F. Broili and J. Schroeder, German authorities on the group, examined the specimen and expressed themselves satisfied with it as a labyrinthodont" (Whitehouse, 1955, p. 56). Since 1955 various ideas have been put forward as to the age of the Marburg Sandstone, with the unquestioned acceptance of *Austropelor* as a labyrinthodont.

It is the purpose of this paper to review the fossil as carefully as possible, in an attempt to throw additional light on the problem of its taxonomic position and perhaps of its age.

At this place I wish to express my appreciation to Mr. Jack T. Woods, Director, and Mr. Alan Bartholomai, Research Curator (Geology), of the Queensland Museum, for the opportunity to prepare further and study the type of *Austropelor*

wadleyi. It was my good fortune to be able to examine *Austropelor* at the Queensland Museum, and to visit its type locality at Lowood[1] in company with Messrs. Woods and Bartholomai. Subsequently Mr. Woods very kindly brought the specimen to New York, on the occasion of a visit he made to the United States, in order that it might receive additional preparation, ably executed by Mr. Gilbert Stucker of The American Museum of Natural History. And here I have been able to study the fossil in detail and at some leisure.

The photographs that illustrate the type of *Austropelor wadleyi* in this paper were made by Mr. Chester Tarka, and the drawing was made by Mr. Michael Insinna, of the Department of Vertebrate Palaeontology of The American Museum of Natural History.

A Reconsideration of the Type of *Austropelor wadleyi*

This fossil, Queensland Museum No. F2628, consists, as Longman pointed out, of three conjoined pieces, the combined length of which is slightly less than 100 mm. On one side the bone is heavily rugose, this rugosity characterized by longitudinal striations and ridges. On the other side the bone is smooth. Along one edge of the bone, between its rugose and smooth sides, is a series of closely set alveoli of comparatively small size, transversely broad as compared with their longitudinal dimensions. There are some 18 alveoli, none of which contains teeth, but all of which are shallow, their basins being filled with cancellous bone. On the rugose side there is a sharp edge running along the borders of the alveoli, and below this edge at a distance of about 8 mm is a very heavy longitudinal ridge. On the smooth side the bone is convex beyond the margins of the alveoli, this convexity merging into a slight longitudinal concavity that occupies the length of the bone near the margin opposite the alveoli. This margin of the bone is rounded, and marks the juncture, opposite the alveoli, between the rugose and smooth sides of the bone. It is a natural border, and shows little breakage.

The form of the bone, its heavy rugosities on one side, and the closely set, transversely broadened alveoli, filled with cancellous bony tissue, are typically labyrinthodont. No other tetrapod jaw would seem to fulfill these characters. The possibility that the fragment might be a portion of a crocodilian jaw was, for instance, considered. But the rugosities are too heavy for a crocodilian jaw of this size, and the alveoli do not accord with what might be expected in a crocodilian bone. For in the crocodilians, and in the archosaurians in general, the alveoli are round or even longitudinally extended, and they are open, not filled by cancellous bone. In short, the form and structure of the alveoli in *Austropelor wadleyi* are of the type that is characteristic for the implantation of labyrinthine teeth.

[1] During the prosecution of studies on Triassic tetrapods, supported by a grant (NSF—G23751) from the National Science Foundation.

Longman identified the fragment as the portion of a right maxilla, from that part of the skull in the vicinity of the narial opening. "On the median border of the upper surface the contours are disrupted for two-thirds of the length where the fragment was broken off from the cranial roof. The remaining third presents a smooth surface which apparently represents the narial opening" (Longman, 1941, p. 30). If such is the case, then this fragment represents a very large skull indeed, because the entire smooth or inner portion of the bone, a natural surface, shows little antero-posterior curvature, and thus would indicate a nasal opening of enormous size—much larger proportionately than is characteristic of other labyrinthodonts. Furthermore, the bone is too narrow to be from the border of the palatal vacuity (which is large in these animals) and in addition there is lacking a secondary row of teeth that would be expected from such a location. Longman thought that the longitudinal ridges on the bone were a part of the system of mucous canals, so typical of labyrinthodonts.

It is here maintained that Longman was mistaken in his morphological identification of the bone. The fossil is not part of a skull, but a portion of a left mandibular ramus. The rugose surface of the bone does not show any indications of a mucous canal system, as Longman thought; rather these rugosities are of the irregular type characteristic for the external surface of a labyrinthodont mandible, as may be seen by comparison with other labyrinthodont lower jaws. The single row of alveoli, bordered internally by a robustly convex region, forming the upper portion of the internal or lingual surface of the mandible, also is typical for a labyrinthodont lower jaw. Indeed, the cross-section of the bone can be matched to a considerable degree by cross-sections in other labyrinthodont rami.

This new identification of the type of *Austropelor wadleyi* as the segment of a left mandibular ramus rather than a portion of a maxilla, as originally determined by Longman, in no way affects the assignment of the fossil to the Labyrinthodontia. Moreover, it confirms the opinion of Broili and Schroeder, as cited by Whitehouse, as to the general zoologic relationships of the specimen. The larger taxonomic implications of the fossil thus remain unchanged.

The Possible Taxonomic Relationships of *Austropelor*

Where is *Austropelor wadleyi* to be placed within the Labyrinthodontia? This question is not easily answered, because the type specimen is so very incomplete that it has few features on which to base any detailed comparisons.

The genus *Austropelor* is not included in Case's study of the Stegocephalia of 1946. In Romer's monograph of 1947 on the Labyrinthodontia it is mentioned in two places as a very problematical form. Von Huene places it, under the name of *"Australopelor"*, within the Metoposauridae in his volume on the lower tetrapods, published in 1956. In the very comprehensive compendium on the lower tetrapods, published in 1964 under the editorship of Orlov, Shishkin proposes that *Austropelor*

is a questionable synonym of *Paracyclotosaurus,* which, of course, brings it within the Cyclotosauridae. In accordance with this conclusion the Cyclotosauridae are shown in a table, on page 65 of the above-mentioned volume, as extending from the beginning of the Middle Triassic through the Lower Jurassic. Other authors who have had occasion to consider *Austropelor* have done so without going into the problem of its exact relationships.

In view of the trends of a labyrinthodont evolution, it seems overwhelmingly probable that *Austropelor* is a stereospondyl. Within the Stereospondyli it would furthermore seem that, tenuous though the evidence may be, the best clues as to the relationships of *Austropelor* are to be found in the relationship of the size of the teeth to the mandibular ramus, and in the cross section of the ramus. In these respects it shows some resemblances to *Eupelor,* for example. In both of these

TABLE 1

COMPARISON OF MEASUREMENTS OF MANDIBULAR RAMI

Species	Depth (mm)	Breadth (mm)	Alveoli per 50 mm	Ratio, breadth/ depth	Alveoli to jaw depth
Austropelor wadleyi QM No. F2628	33·5*	22·0*	9	60	6/33·5
Paracyclotosaurus davidi AMNH No. 8252 (cast) ..	48·0*	44·5*	9	93	8/48
Eupelor fraasi AMNH No. 2994	43·5	24·5	7	56	6/43·5

* Anterior part of ramus.

genera the depth of the mandibular ramus is appreciably greater than its breadth, the measurements in *Eupelor* being taken at a point not far behind the symphysis. In *Paracyclotosaurus* the breadth of the ramus nearly equals its depth in this same portion of the jaw, and this relationship of jaw depth to breadth in its anterior portion is seen in *Parotosaurus,* as recently figured by Welles and Cosgriff (1965). In these latter two genera the depth of the jaw anteriorly is about equal to the space occupied by eight teeth, whereas in *Austropelor* and *Eupelor* the comparable depth of the jaw is equivalent to the space occupied by six teeth. In other words, the teeth of *Austropelor* and *Eupelor* are relatively somewhat larger than they are in *Paracyclosaurus* and *Parotosaurus.*

On the basis of this evidence it is here maintained that *Austropelor* certainly is not to be considered as another species of *Paracyclotosaurus,* nor is it very likely a member of the Capitosauridae. It seems more probably a brachyopid labyrinthodont, and possibly a metoposaur, as indicated by von Huene in 1956.

Two other Australian labyrinthodonts should be considered in the light of any possible taxonomic connections they might have with the fossil now being discussed, especially since they are both brachyopids. These are *Bothriceps australis* and *Platyceps wilkinsoni.*

The first of these two forms is based upon a small skull, in which much of the bone is eroded away, with a closely conjoined lower jaw. The specimen was collected many years ago, and its geologic horizon and locality are unknown. Because of the small size of the specimen, *Bothriceps* is not readily comparable with *Austropelor.* Of course, this might be a juvenile individual, but the skull has the appearance of a fully developed animal, which makes it seem unlikely as a close relative of *Austropelor.* Moreover, lack of stratigraphic and locality records for this specimen makes it almost valueless in this connection.

The type of *Platyceps,* a larval animal, with gill arches preserved, is from the Narrabeen Formation of early Triassic age. Because of its nature and age, it cannot be compared with *Austropelor.*

The Geologic Age of *Austropelor*

The crucial problem as to the age of *Austropelor wadleyi* must now be faced. Does this fossil represent a persistence of the labyrinthodonts (and if so, the only known record) into Jurassic time?

The type fossil was found in a block of Marburg Sandstone, in the bed of the Brisbane River, about one mile south-east of Lowood Railway Station. Although the rock containing the fossil was not in place, there can be no doubt as to its identity as of the Marburg Sandstone. The river bed at this locality is filled with such blocks which have fallen down from banks and cliffs, composed of the Marburg Sandstone bordering the river.

The age of the Marburg Sandstone has been variously interpreted. This sandstone, of varying composition, and strongly cross-bedded, rests on sandstones of the Bundamba Group, and is overlain by the Walloon Coal Measures. In the type description of *Austropelor wadleyi* a section on the age of the "bone-bearing sandstone at Lowood", written by Dr. F. W. Whitehouse, indicates all three of the rock groups referred to by him as *series*—Bundamba, Marburg and Walloon—to be of Jurassic age. "Sufficient it is to say that these three series (Bundamba, Marburg and Walloon) are Jurassic in age and that the Marburg Series which has this bone bed may be placed tentatively about the middle of the period" (Whitehouse in Longman, 1941, p. 32).

As mentioned above, Whitehouse, in 1955, revised this opinion and placed the Marburg Sandstone definitely within the Upper Triassic because of the presence in it of a labyrinthodont amphibian. Hills, in his brief review of Australian fossil vertebrates published in 1958, mentioned *Austropelor* as among the Jurassic tetrapods of this continent.

It is now generally maintained that the Bundamba Group is of Upper Triassic age, while the Walloon Coal Measures are to be placed within the Lower Jurassic (see Cameron et al., 1960). Where then is the intervening Marburg Sandstone to be placed? De Jersey, in the above publication, was rather noncommittal. "However, the general similarity of the microfloras [of the Marburg and Walloon] suggests that there is no major time break between the two formations. Consequently, on the basis of the Lower Jurassic age suggested below for the Walloon Coal Measures, the Marburg Sandstone would be either late Triassic or early Jurassic" (de Jersey, in Cameron *et al.*, 1960, p. 291). This same author has, however, more recently come to the conclusion that, upon the basis of paleobotanical evidence as well as upon the established conformable relationships above and disconformable relationships below it, the Marburg Sandstone should be closely associated with the overlying Jurassic Walloon Coal Measures rather than with the underlying Triassic Bundamba Group.

" . . . the occurrence of *Classopollis* down to the lowest known outcrop of the formation at Lowood is strong evidence for placing the whole of the Marburg Sandstone in the Jurassic. The Jurassic age of the formation is further indicated by the presence of forms . . . which are known from Jurassic sediments elsewhere, but have not been found in the Triassic."

"This microfloral evidence of a Jurassic age is in conflict with the conclusions of Whitehouse (1955) who suggested an Upper Triassic age for the formation . . . based on the occurrence of a jaw fragment of a Labyrinthodont in the Marburg Sandstone . . . Whitehouse considered that the absence of Labyrinthodonts from the post-Triassic sediments elsewhere indicated that the Marburg Sandstone could not be younger than Upper Triassic. In the writer's opinion, greater reliance should be placed on the microfloral evidence of a Jurassic age than that of this isolated bone fragment, and the possibility must be considered that the jaw fragment in question, if correctly identified, may be a re-worked fossil from underlying Triassic sediments" (de Jersey, 1963, p. 14).

These conclusions have been recently strengthened, as the present writer is informed by Mr. Woods, by palynological studies as yet unpublished. There seems indeed little reason on the basis of the abundant evidence now at hand to question the Jurassic age of the Marburg Sandstone.

In view of the undoubted taxonomic position of *Austropelor wadleyi* within the Labyrinthodontia, and the almost certain position of the Marburg Sandstone within the Jurassic sequence in Queensland, serious consideration must therefore be given

to the suggestion by de Jersey (which has been made by other authorities as well) that the fossil is a re-worked specimen from underlying Triassic sediments. This solution of the problem is hereby proposed, even though it involves certain difficulties. For instance, in a letter to the present writer Mr. Woods has stated that "I would expect remané material to have to be mineralized more extensively to survive any considerable transport during the deposition of such sands." Yet in spite of this qualification, the occurrence of the single type specimen of *Austropelor wadleyi* as a re-worked fossil seems the most logical explanation for its presence in the Marburg Sandstone. Such an interpretation is in accordance with all present records of labyrinthodont stratigraphic relationships. There will have to be more definite evidence than is afforded by the single specimen of *Austropelor wadleyi* to justify the extension of the labyrinthodont amphibians into Jurassic sediments.

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