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New observations on the snouts of rhizodont fishes (Palaeozoic Sarcopterygii)

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Abstract – Reinvestigation of the snout of the Lower Carboniferous rhizodont fish *Barameda decipiens*, together with observations on an isolated premaxilla of *Strepsodus sauroides* from Scotland and a new Devonian rhizodont from Canowindra, Australia, reveals that the rhizodontid snout had only one pair of nostrils rather than two as previously suggested. There are distinct lateral rostral and tectal bones surrounding the external naris. The palate of *Barameda* also shows evidence of a choana being present. The protrusion of the lower jaws in *Barameda*, previously interpreted as an artefact of preservation, is matched in the three-dimensional Canowindra material and appears to be a real morphological feature. These data permit a new reconstruction of the head of *Barameda*.

INTRODUCTION

The first rhizodontid sarcopterygian to be described from relatively complete cranial remains was the Early Carboniferous *Barameda decipiens*, from Mansfield, Victoria, Australia (Long 1989), although a partial head of a juvenile of ?*Strepsodus anculonamensis* from the Early Carboniferous of Foulden, Scotland, had been reported by Andrews (1985). Long (1989) concluded that *Barameda* had two pairs of external nares, rather than the single pair seen in all osteolepiform, elpistostegid (= panderichthyid; Schultze 1996) fishes and tetrapods. Andrews (1985) had tentatively reconstructed ?*Strepsodus* with two pairs of external nares, so Long concluded that this condition was general for rhizodonts. As two pairs of external nares is the primitive condition within the Osteichthyes, Long was prompted to place rhizodonts below osteolepiforms and elpistostegids in the tetrapod stem group.

New work on British Carboniferous rhizodontids, by J.E. Jeffery at the University of Cambridge Museum of Zoology, together with the recent discovery of a primitive rhizodontid in the Late Devonian Canowindra site in New South Wales (Johanson 1997; Johanson and Ahlberg 1998), prompted us to restudy the snout of *Barameda*. The original interpretation by Long was based on examination of several latex casts of the skull of NMV P160880 (in the vertebrate palaeontological collection of the Museum of Victoria, Melbourne), in which the exact pattern of the snout bones was not clear.

We took the opportunity to examine a well-preserved natural mould of a premaxilla of *Strepsodus sauroides* (Binney, 1841) from Airdrie, Scotland (BMNH P364(2), in the vertebrate palaeontological collection of the Natural History Museum, London), which clarified the sutural relationships of this bone to surrounding elements. The information from this specimen and the Canowindra rhizodontid has allowed us to reinterpret the snout pattern and cranial morphology of NMV P160880, and produce a new skull reconstruction for *Barameda* (see Figure 4).

THE SNOUT OF RHIZODONTIDS

In Long's (1989) description of *Barameda*, the anterior nostril was shown as bounded ventrally by the premaxilla, mediodorsally by the anterior supraorbital (= prefrontal in tetrapod terminology), and dorsolaterally by the supraorbitotectal (SO-Te element of Long 1989, figure 2). The posterior nostril was placed in the anteroventral corner of the orbit, its position indicated by a notch in the dorsal margin of the lacrimal bone. It was described as being bordered anterodorsally by the supraorbitotectal bone and posterodorsally by the orbit (Long 1989, figures 2, 5). The position of the posterior nostril thus differed from that inferred by Andrews (1985) for ?*Strepsodus*, but resembled that in primitive actinopterygians (Gardiner 1984). However, the material was in part difficult to interpret. Long (1989: 4) stated that "the position of the external nostrils is not clearly seen on NMV P160880 but can be estimated from the notches in the premaxilla and lacrimal bones".

The anterior naris identified by Long (1989) is indubitably real (Figure 1). However, it is not as previously described located in a notch in the

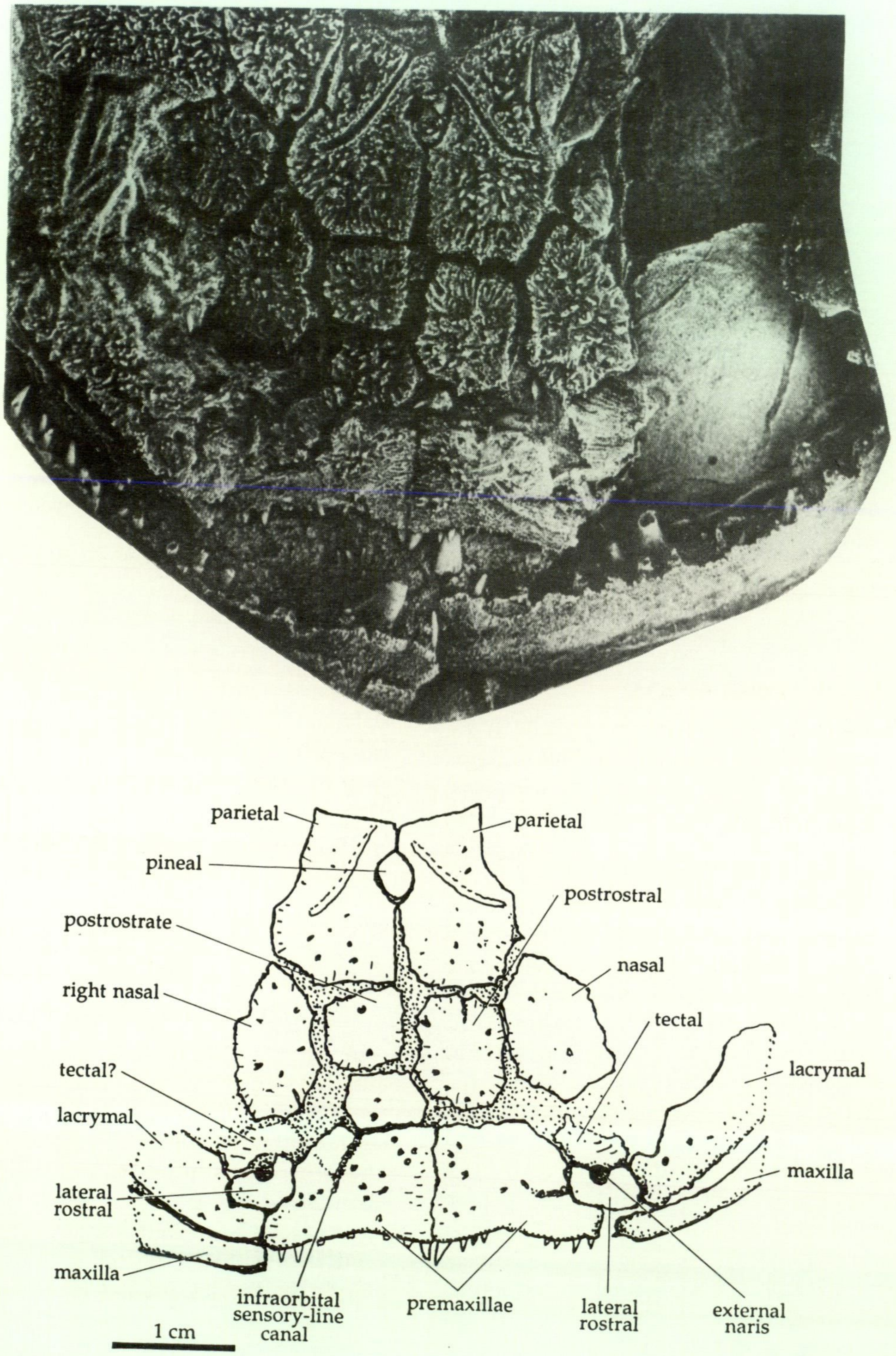

Figure 1 The snout of *Barameda decipiens*, NMV P160880. A, latex cast whitened with ammonium chloride showing actual arrangement of bones. B, new interpretation of snout bones. Note the protruding lower jaws shown in A.

premaxilla, but is bounded ventrally by a lateral rostral bone. The recognition of this fact was prompted by our examination of the premaxilla of *Strepsodus sauroides* (Figure 2), which clearly lacks a narial notch but has a large overlap area that presumably (by analogy with osteolepiforms) received the lateral rostral and part of the tectal. Re-examination of NMV P160880 showed that a lateral rostral was present on both sides of the specimen, but that Long (1989) had interpreted its suture with the premaxilla as a collapse crack over the infraorbital sensory-line canal. This sensory line

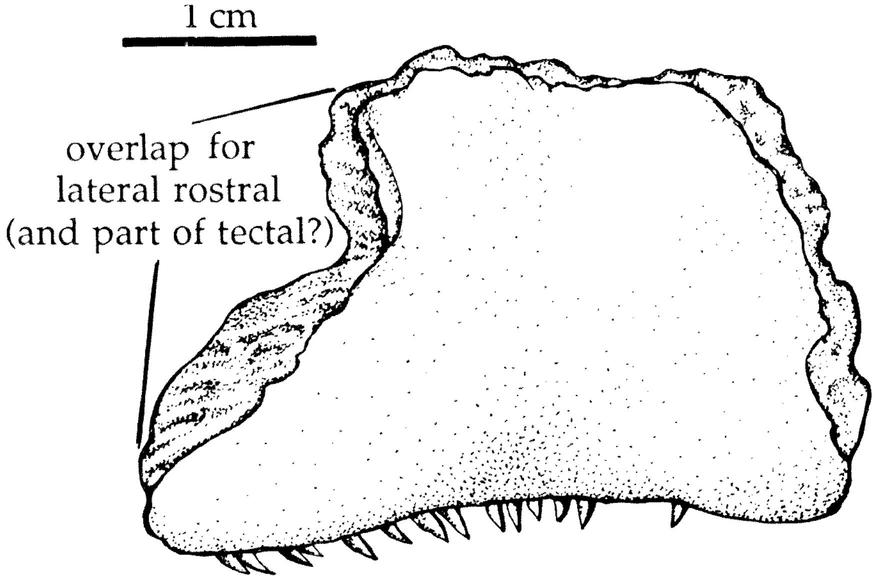

Figure 2 Premaxilla of *Strepsodus sauroides*, BMNH P364(2) from Airdrie, Scotland, showing contact margins for lateral rostral and possibly part of the tectal.

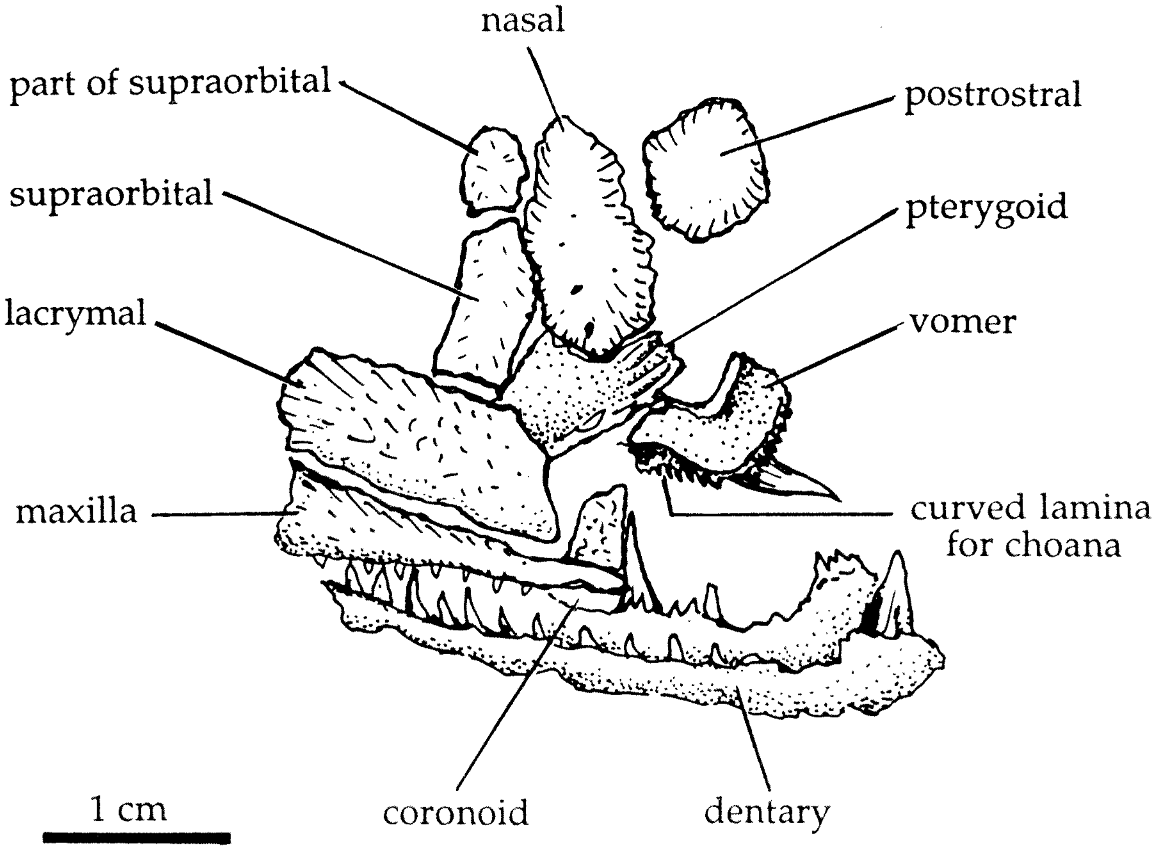

Figure 3 Sketch based on photograph of an early preparation of NMV P160880 showing the vomer having a curved lamina for the choana.

canal is in fact still visible as a shallow groove within the premaxillae, anterior and ventral to the lateral rostral. The dorsal boundary of the naris is less easy to interpret, as the skull is disrupted in this region on both sides, but a poorly preserved tectal can be identified dorsal to the naris on the left side of the skull. The arrangement of circumnarial bones thus seems to be identical to that in osteolepiforms (e.g. *Eusthenopteron, Glyptopomus*, Jarvik 1966, figure 14). This is also true in the new rhizodont from Canowindra (Johanson and Ahlberg 1998).

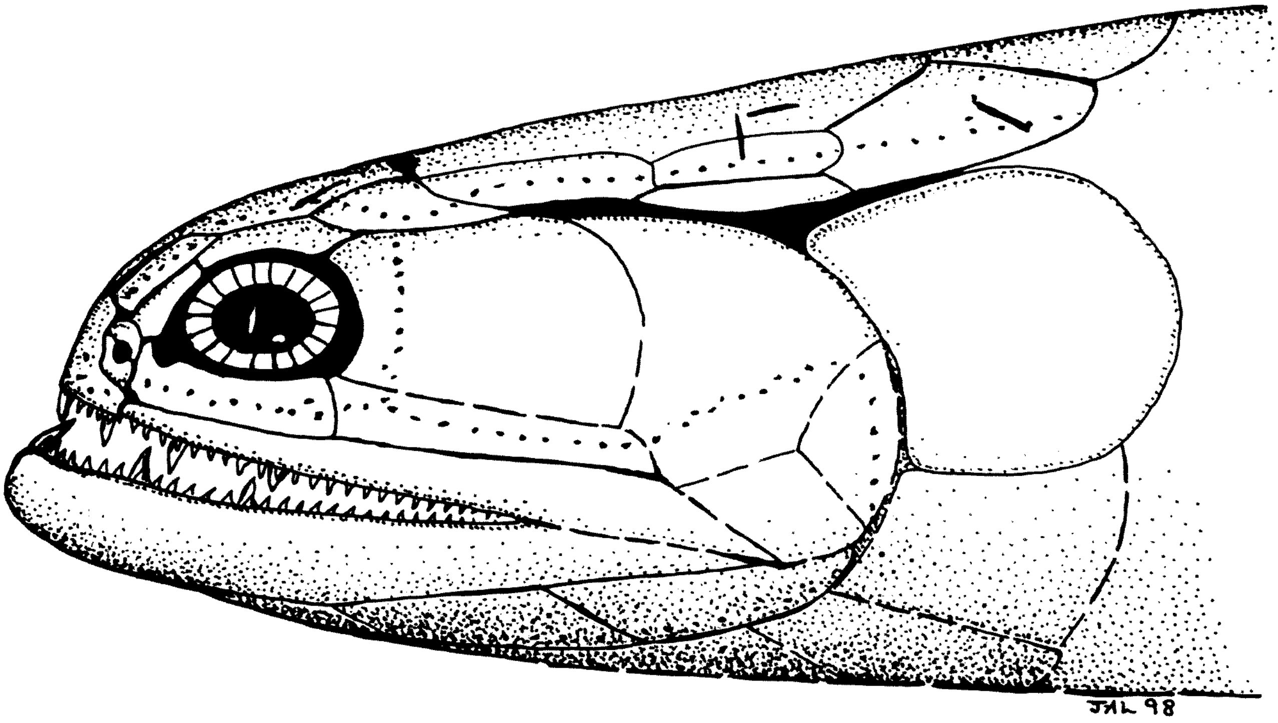

Figure 4 New reconstruction of the head of *Barameda decipiens* in lateral view.

A 'posterior naris' of *Barameda* was interpreted as being present by Long (1989, figure 3), based on a single notch seen on the right lachrymal. As mentioned above, its supposed position corresponds approximately to that in primitive actinopterygians (Gardiner 1984). Unlike the anterior naris, which is quite deep and easily recognized on both sides of the skull, the 'posterior naris' notch is shallow and poorly defined. This is even more true of the supposed 'posterior naris' of ?*Strepsodus* (Andrews 1985).

The new rhizodontid from Canowindra has a well preserved narial region, and quite clearly lacks a posterior naris (Johanson and Ahlberg 1998). Given the poor quality of evidence for such a nostril in *Barameda* and ?*Strepsodus*, we conclude that these genera most probably also have a single pair of nares.

Latex casts representing the initial stage of preparation on the head of NMV P160880 show that the vomers and part of the palate were exposed in dorsal view before the skull was fully prepared to reveal the level of the skull roof (by negative preparation, removing the rock to reveal the impression of the bones). One of these casts has been illustrated here (Figure 3) to demonstrate the presence on the vomer of a curved descending lamina of bone and a gently embayed lateral margin bounded anteriorly by a blunt process. This embayed margin is clearly the border of the choana, as seen in the vomers of osteolepiform fishes (e.g. *Gogonasus*, Long *et al.*, 1997; *Eusthenopteron*, Jarvik, 1980).

In the articulated specimen of *Barameda* illustrated by Long (1989, figures 1, 2) the lower jaws protrude much further than the upper jaw margins shown by the limits of the margins of the premaxillae. This was originally interpreted as a preservational artefact, but as the same condition can be observed in both flattened and fully three-dimensional specimens of the new rhizodontid from Canowindra (Johanson and Ahlberg 1998) we have reinterpreted it as a real morphological feature. It may indicate either a possible close affinity between these two taxa, or be a general feature of rhizodontids. Functionally, it may be related to a life as a benthic ambush predator; a similar morphology is seen in the living anglerfish *Lophius*. Based on the new information on the snout and lower jaws of *Barameda*, we have attempted a new reconstruction of the head (Figure 4).

DISCUSSION

The Rhizodontida are a monophyletic group, distinguished by a unique pectoral fin morphology with long unjointed lepidotrichia, and complex overlaps between cleithrum and clavicle (Andrews 1985; Long 1989; Johanson and Ahlberg 1998, Ahlberg and Johanson 1998). In the recent analysis of sarcopterygian interrelationships by Cloutier and Ahlberg (1996), based on 140 characters and 158 apomorphic character states, the Adams and strict consensus trees placed the Rhizodontida (based on data from *Barameda* and *Strepsodus* spp.) as the plesiomorphic sister group to the Osteolepidida + Elpistostegalia + Tetrapoda. Within this clade, Cloutier and Ahlberg (1996: 467) noted that "the Tetrapodomorpha share a single external naris which corresponds to the anterior naris, however the condition is unknown in the Rhizodontida." The new information on the snout reinforces this view that the Rhizodontida is a group within the Tetrapodomorpha. Although they appear more tetrapod-like than hitherto recognized, in possessing a single pair of nares and a choana, they are nevertheless probably basal members of the Tetrapodomorpha (Johanson and Ahlberg 1998, Ahlberg and Johanson 1998).

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