The phylogeny of rhynchosaurs (Reptilia: Diapsida: Triassic), and two new species.

M.J. Benton (Belfast, Northern Ireland).

The rhynchosaurs are a group of small to medium-sized herbivorous reptiles known from the Triassic of most parts of the world (Chatterjee 1980; Benton 1983). About twelve genera have been described, some based on rather limited material. The relationships of rhynchosaurs within Diapsida have been controversial, and there are also two very different current schemes of relationships of genera within the group. The aims of this paper are to present a cladistic analysis of Rhynchosauria, and to give outline descriptions of two new forms from England.

The place of Rhyncho sauria within Diapsida

Until recently, most authors classed the rhynchosaurs with the sphenodontids in Rhynchocephalia (e.g. Romer 1966). This viewpoint was questioned by a number of authors more recently (reviewed Carroll 1977; Brinkman 1981), and several independent cladistic analyses now place the rhynchosaurs in an archosauromorph branch of the Diapsida, in association with prolacertiforms and archosaurs (e.g. Benton 1983, 1984a, 1985; Evans 1984; 1986; Gauthier 1984; Chatterjee 1986).

Within the Archosauromorpha, the Rhynchosauria have been placed in three positions (Fig. 1.) either as the second most primitive sister group, after *Trilophosaurus* (Benton 1984a, 1985), as more primitive than *Trilophosaurus* (Evans 1983), or as a close sister-group of *Trilophosaurus* (Chatterjee 1986). There is no space here to discuss the validity of these three hypotheses of relationship, other than to question Chatterjee's model. He lists three supposed synapomorphies of Rhynchosauria and *Trilophosaurus*:

(1) ankylothecodont tooth implantation;
(2) premaxilla and anterior part of dentary edentulous;
(3) parietal with a strong median crest.

However, if *Mesosuchus* is accepted as a rhynchosaur (see below), it lacks characters (1) and (2), and character (3) is not clear. *Trilophosaurus* is so bizarre in many respects (it is a "diapsid" with only one temporal opening, after all), and the suggestion of a relationship with Rhynchosauria is intriguing.

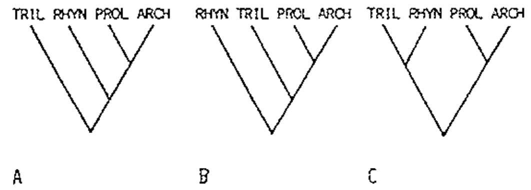

Fig. 1. Three views of the cladistic relationships of Rhynchosauria (RHYN) to *Trilophosaurus* (TRIL), Prolacertiformes (PROL), and Archosauria (ARCH). A, after Benton 1984, 1985; B, after Evans 1988; C, after Chatterjee 1986.

Relationships of Rhynchosauria

There are currently about 12 genera, and 17 species of rhynchosaur listed by various current authorities (e.g. Dutuit 1976; Chatterjee 1980; Benton 1983; Buffetaut 1983; Murry 1986) (see Table 1). Many of these taxa are represented by only fragmentary remains. The early "rhynchosaur" *Noteosuchus* lacks many diagnostic parts and it is not considered here (Benton 1985).

In constructing a cladogram of rhynchosaur relationships, only seven taxa could be used with any confidence:the early forms *Mesosuchus* and *Howesia*, and *Stenaulorhynchus*, *Rhynchosaurus articeps*, *Scaphonyx fischeri*, *Hyperodapedon gordoni*, and *H. huxleyi*. A data matrix was constructed in which 24 characters were assessed from specimens and from the literature (key references listed by Chatterjee 1980 and Benton 1983). Polarity was determined by comparison with an outgroup of "other early diapsids" (*Claudiosaurus*, *Petrolacosaurus*, *Prolacerta*, *Thadeosaurus*, *Youngina*). This data matrix gave rise to a single largely consistent cladogram (Fig. 2), with only three homoplasies (nos. 17-19 in *Mesosuchus*). It is not certain whether synapomorphy 3 (beak-like toothless premaxilla), characteristic of Rhynchosauridae, was present in *Howesia* or not.

The remaining nine taxa were assessed for synapomorphies, as far as possible and added to the core cladogram. *Acrodenta* could not be placed, *Mesodapedon* and the Warwick and Devon rhynchosaurs fall in the "Rhynchosaurie" group, and the other five in the "Hyperodapedontine" group. However, several of these taxa (*Mesodapedon*, *Acrodenta*, *Isalorhynchus*, *Supradapedon*, *Scaphonyx sanjuanensis*) appear to lack diagnostic characters, while others (Texas, Nova Scotia, Warwick and Devon rhynchosaurs) have yet to be described. Data on the two American forms have been gleaned from published scources (Chatterjee 1980; Murry 1986), while data on the two English forms have been obtained from unpublished descriptions new specimens (Benton, in prep.). The Warwick and the Devon rhynchosaurs are briefly characterised below.

Table 1
The taxa of rhynchosaurs, arranged in approximate stratigraphic order. Da from Dutuit (1976), Chatterjee (1980), Benton (1983), Buffetaut (1983) and Murry (1986).

Early Triassic

Mesosuchus browni, *Cynognathus* Zone, South Africa.
Howesia browni, *Cynognathus* Zone, South Africa.

Middle Triassic

Stenaulorhynchus stockleyi, Manda Formation, Tanzania.
Mesodapedon kuttyi, Yerrapalli Formation, India.
Rhynchosaurus articeps, Tarporley Siltstone Formation, England.
"Warwick rhynchosaur", Bromsgrove Sandstone Formation, England.
"Devon rhynchosaur", Otter Sandstone Formation, England.

Late Triassic

?*Acrodenta irerhi*, Argana Formation, Morocco.
Isalorhynchus genovefae, Isalo II Formation, Madagascar.
Scaphonyx fischeri, Santa Maria Formation, Brazil.
Scaphonyx sanjuanensis, Ischigualasto Formation, Argentina.
"Texas rhynchosaur", Dockum Group, USA.
"Nova Scotia rhynchosaur", Wolfville Formation, Canada.
Hyperodapedon gordoni, Lossiemouth Sandstone Formation, Scotland.
Hyperodapedon huxley, Maleri Formation, India.
Supradapedon stockleyi, ?Upper Triassic, Tanzania.

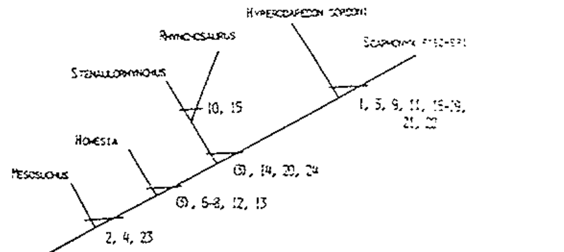

Fig.2. Most parsimonious cladogram showing the relationships of the seven best-kno taxa of rhynchosaurs. Synapomorphies 1-24 are : 1, skull broader than long. 2, premaxilla with a small number or no, acrodont teeth; 3, premaxilla beak-like an with no teeth; 4, single median naris; 5, jugal occupies a large area of the cheek, being broader than the maxilla; 6, frontal is shorter than the parietal; parietals fused; 8, parietal foramen absent; 9, loss of supratemporal; 10, occip tal condyle placed well in front of quadrates; 11, lower jaw is very deep: depth is one-quarter to one-third of the length; 12, teeth are ankylothecodont; 13, ba teries of teeth on maxilla and dentary; 14, interlocking blade and groove jaw apparatus; 15, two grooves or maxilla, two ridges on dentary; 16, single groove maxilla, single ridge on dentary; 17, no teeth on lingual side of maxilla; 18, dentary with only one or two rows of teeth; 19, one tooth row only on dentary; 2 no teeth on pterygoid; 21, coracoid has no posterior process; 22, femur about th same length as the humerus; 23, three proximal tarsals; 24, centrale is large an closely associated with the astragalus.

Two new English rhynchosaurs

The Warwick rhynchosaur (skull length 90-140 mm, typically 100 mm) is larger than *Rhynchosaurus articeps* (skull length 60-85 mm) (Fig. 3a, b) and differs from it in a few additional respects. The skull is higher in side view, and broader in dorsal view. The jugal in the Warwick form occupies a larger part of the cheek area than in *R. articeps*, and the orbit is placed relatively further forward.

The Devon rhynchosaur, now known from a great deal of new material (Spencer and Isaac 1983) shows the same size range as the Warwick form (skull length 90-150 mm), but there are more specimens at the larger end of the size range (140-150 mm) (Fig. 3c). The Devon rhynchosaur has the same dentition as *Stenaulorhynchus* and *Rhynchosaurus*, but the skull is broader than it is long, a synapomorphy of *Hyperodapedon* and *Scaphonyx* (no. 1), and thus probably a homoplasy here.

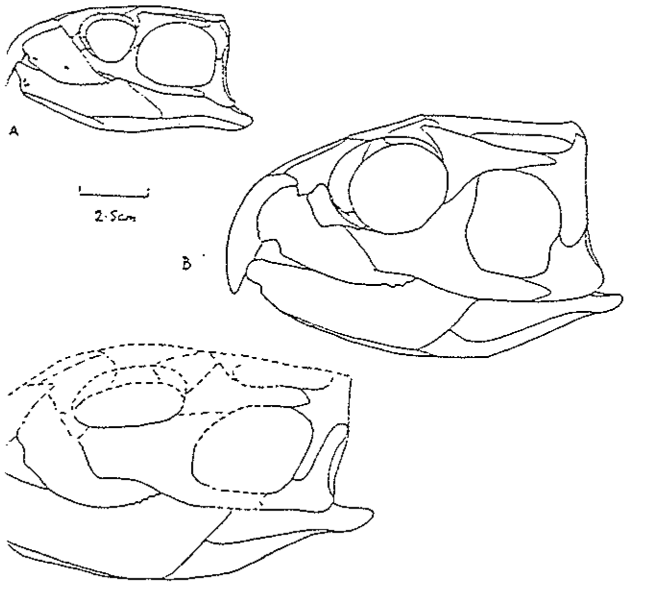

Fig. 3 Restorations of the skulls of the three English rhynchosaurs based on unpublished studies of specimens: A, *Rhynchosaurus articeps*; B, the Warwick rhynchosaur, and C, the Devon rhynchosaur.

Geographic distribution of rhynchosaurs

Rhynchosaur fossils have been collected in Triassic rocks on all continents except Antarctica and Australia. The few major clades in Fig. 2 represent an approximate sequence in stratigraphic terms:

1. *Mesosuchus* Early Triassic;
2. *Howesia* Early Triassic;
3. Rhynchosaurinae Middle Triassic;
4. Hyperodapedontinae Late Triassic.

Age details may be found in Chatterjee (1980), Olsen and Galton (1984), Olsen and Sues (1986) and Benton (1986). From an Early Triassic representation only in South Africa (Fig. 4), rhynchosaurs spread to eastern Africa, India and north-western Europe in the Middle Triassic, and Madagascar, North Africa (?), South America, and North America in the Late Triassic, before their global extinction at the end of the Carnian stage (Benton 1986; Olsen and Sues 1986).

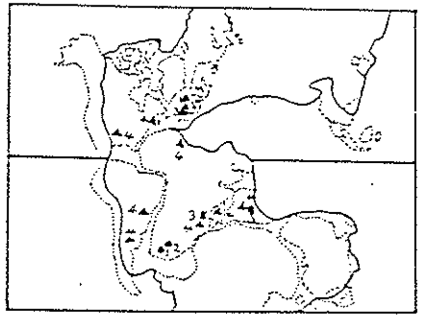

Fig. 4 Palaeogeographic map of the Triassic world with rhynchosaur localities marked. Key: 1, *Mesosuchus* (Early Triassic); 2, *Howesia* (Early Triassic); 3, Middle Triassic forms; and 4, Late Triassic forms.

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