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SHORT COMMUNICATION

ON *FODONYX SPENCERI* AND A NEW RHYNCHOSAUR FROM THE MIDDLE TRIASSIC OF DEVON

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Based mainly on isolated tooth-bearing elements, the rhynchosaur remains from the South Devon coast (Fig. 1) were first noticed in the late 19th century and variously assigned to the genera *Hyperodapedon* Huxley or *Rhynchosaurus* Owen (see review in Benton, 1990). More complete specimens were recovered from the early 1980s onward (Spencer and Isaac, 1983; Benton, 1988, 1990, 1997; Benton et al., 1993, 1994; Hone and Benton, 2008), allowing the recognition of new taxonomic entities (Benton, 1990; Hone and Benton, 2008). The 'Devon rhynchosaur' (Benton, 1988) was initially considered as a new species of the genus *Rhynchosaurus*, *R. spenceri* Benton, 1990, with a partial skull and mandible (EXEMS 60/1985.292) designated as the holotype. More recently, both a partial post-cranium and a nearly complete skull (Benton et al., 1993; Hone and Benton, 2008) were assigned to that species, but following previous interpretations (Wilkinson and Benton, 1995; Langer and Schultz, 2000), Hone and Benton (2008) proposed its inclusion in a new genus, *Fodonyx*.

The aim of this paper is to assign the referred skull of *Fodonyx spenceri* described by Hone and Benton (2008) to a new genus and species. This is important for an accurate estimate of the rhynchosaur diversity of the Otter Sandstone Formation, which may include the most basal members of the two rhynchosaur lineages that further spread during Middle ('stenaulorhynchines') and Late (hyperodapedontines) Triassic times.

Institutional Abbreviations—**BRSUG**, University of Bristol, Department of Geology, Bristol, United Kingdom; **EXEMS**, Royal Albert Memorial Museum, Exeter, United Kingdom; **MCNSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **MCP**, Museu de Ciências e Tecnologia, PUC-RS, Porto Alegre, Brazil; **UFRGS**, Departamento de Paleontologia e Estratigrafia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Anatomical Abbreviations—**a**, angular; **bc**, braincase; **bpp**, basipterygoid process; **bs**, basisphenoid; **bt**, basal tubera; **ch**, choana; **d**, dentary; **ec**, ectopterygoid; **ecp**, ectopterygoid process; **'eo'**, 'exoccipital'; **ep**, epipterygoid; **f**, frontal; **fm**, foramen magnum; **hy**, hyoid; **ic**, interfenestralis crest; **iof**, infraorbital foramen; **j**, jugal; **l**, lacrimal; **m**, maxilla; **md**, mandible; **mf**, metotic foramen; **mg**, meckelian groove; **n**, nasal; **oc**, occipital condyle; **p**, parietal; **pa**, prearticular; **pf**, postfrontal; **pl**, palatine; **pm**, premaxilla; **po**, postorbital; **pop**, paroccipital process; **pr**, prootic; **prf**, prefrontal; **pt**, pterygoid; **q**, quadrate; **qp**, quadrate process; **sa**, surangular; '**so'**, 'supraoccipital'; **sp**, splenial; **sq**, squamosal; **st**, supratemporal; **v**, vomer.

SYSTEMATIC PALAEONTOLOGY

DIAPSIDA Osborn, 1903
ARCHOSAUROMORPHA Huene, 1946
RHYNCHOSAURIA Osborn, 1903
BENTONYX SIDENSIS, gen. et sp. nov.
(Figs. 2, 3)

Etymology—The generic epithet is in honor of the British palaeontologist, and 'rhynchosaur champion' Michael James Benton, formed with the Greek suffix ὄνυξ (onyx = claw), commonly applied to rhynchosaurs. The specific epithet refers to the Sid River, near the outfall of which the holotype was collected.

Holotype—BRSUG 27200, nearly complete skull, lacking the lower part of the temporal areas and the caudolateral corners, and partial mandible lacking most of the post-dentary bones.

Type Locality and Horizon—Pennington Point (National Grid reference: SY 130873), 20 m west of the Sid River outfall. This is about 3 km west of the cliffs near Peak Hill (NGR: SY 1060 8639), where the type specimen of *Fodonyx spenceri* was collected (Fig. 1). Both sites are representative of the Anisian Otter Sandstone Formation (Benton et al., 1994; Hounslow and McIntosh, 2003).

Diagnosis—Two autapomorphic traits were recognized in *Bentonyx sidensis*, a rounded depression on the ventral surface of the basisphenoid and exceptionally large basal tubera, which support its distinctiveness in relation to all other rhynchosaurs with a preserved braincase. This is not the case of *Fodonyx spenceri*, so that the autapomorphic status of those traits may only be confirmed with additional specimens of *F. spenceri*. Yet, *B. sidensis* differs from that taxon by a narrower caudal margin of the skull (maximum width subequal to total skull length), a slender rostral ramus of the jugal (subequal in depth to the underlying portion of the maxilla), the rostral margin of the quadrate ramus of the pterygoid forming an angle of less than 50° to the sagittal line, and maxillary tooth-bearing plates corresponding to more than half of the palatal length, measured from the rostral tip of the vomer to the caudal margin of the pterygoid (not including the caudal projection of the quadrate ramus).

Comments—Based on the holotype of *Bentonyx sidensis*, Hone and Benton (2008) defined a ventrally angled paroccipital process as diagnostic for *Fodonyx spenceri*. Yet, this trait is not unique to BRSUG 27200, but also present in the 'Mariante rhynchosaur' (UFRGS PV-0168T), as well as in several specimens of *Hyperodapedon* (MCP 4103PV, MCNSJ 680, UFRGS PV-0149T, PV-0132T). Indeed, the inconsistent distribution of the character in that genus further refutes its diagnostic status, and *F. spenceri* requires an emended diagnosis. In the absence of any obvious autapomorphy, *F. spenceri* (EXEMS 60/1985.292) can be

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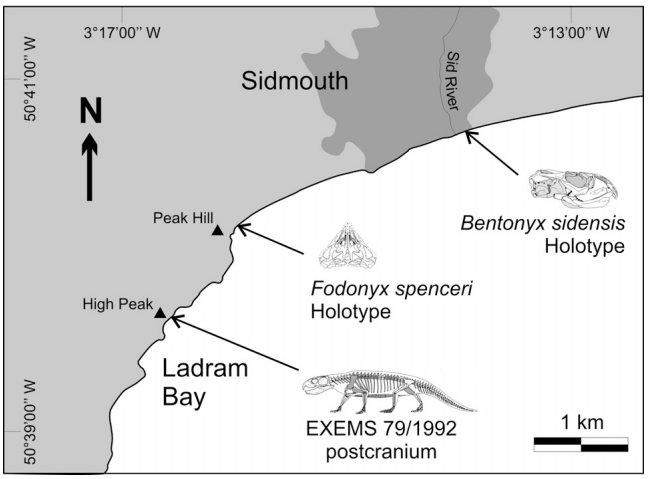

FIGURE 1. Map of the South Devon coast, from Sidmouth to Ladram Bay, depicting the sites where the most complete rhynchosaur specimens of the Otter Sandstone Formation were collected.

differentiated from all other known rhynchosaurs based on the presence of a 'cushion-shaped' lateral tooth bearing area of the maxilla that lacks pyramidal teeth. In addition, *F. spenceri* further possesses a unique combination of features, including a skull broader than long (otherwise known only in Hyperodapedontinae rhynchosaurs), and traits hitherto unrecognized in hyperodapedontines, such as an anguli oris crest that does not reach the rostral margin of the jugal and a lower jaw more than four times longer than high.

RESULTS AND DISCUSSION

Fodonyx spenceri versus *Bentonyx sidensis*

Hone and Benton (2008) referred the two most complete rhynchosaur skulls found in the Otter Sandstone Formation (EXEMS 60/1985.292 and BRSUG 27200) to a single genus and species, *Fodonyx spenceri*. Yet, these two skulls bear a number of differences in their morphology, the most conspicuous of which is the broader caudal margin of EXEMS 60/1985.292 (holotype of *F. spenceri*). The skulls are nearly equal in length (ca. 140 mm), but whereas BRSUG 27200 (holotype of *Bentonyx sidensis*) can be reconstructed with a maximum caudal width of about 130 mm, that of EXEMS 60/1985.292 is nearly 170 mm (Fig. 3). A wider caudal margin of the skull typically characterizes rhynchosaurs of the hyperodapedontine lineage, as does other features of EXEMS 60/1985.292, such as a larger jugal and a more laterally directed quadrate ramus of the pterygoid. In fact, aside from caudally broader, skulls of hyperodapedontine rhynchosaurs are also deeper. This condition is reflected in the shape of the jugal, which occupies a larger portion of the cheek area. Although not entirely preserved in either skull, the size of the jugal can be estimated based on the depth (dorsoventral) of the rostral ramus of the bone. In EXEMS 60/1985.292 (Benton, 1990:fig. 28a), the base of that ramus is about twice that of the underlying portion of the maxilla (lateral view), whereas in BRSUG 27200 these are nearly equal in depth (Fig. 2B). Indeed, as reconstructed by Benton (1990) for EXEMS 60/1985.292, the caudal depth of the skull accounts for half of its length, whereas that relation is slightly over 30% in BRSUG 27200. Besides, in the palatal area of EXEMS 60/1985.292, the rostral margin of the quadrate ramus of the pterygoid forms an angle of about 55° to the sagittal line. On the other hand, as expected in a caudally narrower skull, that angle is 45° in BRSUG 27200. Indeed, the type specimens of *F. spenceri* and *B. sidensis* are not only notably different, but the former shares derived traits with hyperodapedontine rhynchosaurs.

An increase in the caudal skull breadth has been variously suggested as constrained by the ontogeny of hyperodapedontine rhynchosaurs (Barberena, 1971; Benton and Kirkpatrick, 1989; Azevedo and Cavalcanti, 2002). The implications of this hypothesis have to be considered, given that the most evident difference between EXEMS 60/1985.292 and BRSUG 27200 relies on the narrower skull of the latter. Yet, the rough skull surface of BRSUG 27200, with depressions in the prefrontal, frontal, jugal, and postorbital, and rugose crests in the lacrimal, prefrontal, and postfrontal, is reminiscent of that seen in mature individuals of various amniote groups (Mook, 1921; Barry, 1957; Hill et al., 2003; Vasconcelos and Carvalho, 2005), a pattern that possibly results from the accumulation of bone resorption-reconstruction cycles (Buffrénil, 1982). In addition, both specimens are nearly equal in cranial length, weakening the hypothesis that BRSUG 27200 represents a young or sub-adult of *Fodonyx spenceri*. Regardless, the only comprehensive study of rhynchosaur ontogeny (Benton and Kirkpatrick, 1989) failed to recognize a positive allometric growth in the overall caudal width of the skull. Therefore, there is no reason to consider the anatomical differences between BRSUG 27200 and EXEMS 60/1985.292 as the result of ontogenetic variation within a single taxon.

Phylogenetic Position of the Devon Rhynchosaurs

In the phylogenetic analyses of Hone and Benton (2008), the scoring of all specimens referred by those authors to *Fodonyx spenceri*, or the holotypic skull alone, equally resulted in its placement as the sister taxon to *Ammorhynchus navajoi* plus Hyperodapedontinae. In the updated study of Montefeltro et al. (2010), the 'Devon rhynchosaur' (labeled as *F. spenceri*) was scored based on both the more complete skull (BRSUG 27200) and the post-cranium (EXEMS 79/1992), and was found to represent the sister group to Hyperodapedontinae. Yet, the recognition that two unique rhynchosaur taxa are represented by isolated skull specimens from the Otter Sandstone Formation renders the unambiguous association of the post-cranium EXEMS 79/1992 to either *F. spenceri* or *Bentonyx sidensis* unfeasible. A topotypic criterion is also not applicable, given that EXEMS 79/1992 comes from a site different from those that yielded the skulls (Fig. 1).

In a first attempt to define the phylogenetic position of *Bentonyx sidensis*, the post-cranial character scored for '*Fodonyx spenceri*' were excluded from the data matrix of Montefeltro et al. (in press), and the analysis was conducted with the same parameters employed by those authors. This resulted in two most parsimonious trees (MPT) of 93 steps (Fig. 4A), in which *B. sidensis* is placed either at the stem of the hyperodapedontine lineage, as the sister taxon to a clade composed of *Isalorhynchus*, *Teyumbaita*, and *Hyperodapedon*, or as the basal-most taxon of a Middle Triassic rhynchosaur radiation (the 'stenaulorhynchines'), that also includes *Stenaulorhynchus stockleyi*, from the Anisian Manda beds of Tanzania (Huene, 1938; Abdala et al., 2005; Nesbitt et al., 2010) and the so-called 'Mariante-rhynchosaur' from putatively Ladinian strata of the Santa Maria Formation of south Brazil (Schultz and Azevedo, 1990; Langer et al., 2007). Subsequently, the holotypic skull of *F. spenceri* was added to the data matrix (Table 1). This analysis also resulted in two MPTs (94 steps), in which *F. spenceri* is placed as the sister taxon to Hyperodapedontinae. As in the first analysis, *B. sidensis* has a dubious position as the sister taxon of either *S. stockleyi* plus 'Mariante-rhynchosaur,'

TABLE 1. Character state scores for *Fodonyx spenceri* (EXEMS 60/1985.292); line inserted into the data matrix of Montefeltro et al. (2010).

10	20	30	40	50	59
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or *F. spenceri* plus Hyperodapedontinae. In any case, the different phylogenetic placements of the rhynchosaur skulls from the Otter Sandstone Formation strengthen the hypothesis that these specimens do not belong to a single taxon. The results of the analyses also suggest that *F. spenceri* is more derived than *B. sidensis* in the direction of Late Triassic rhynchosaurs, a position also supported by traits shared with Hyperodapedontinae.

CONCLUSIONS

The two best preserved rhynchosaur skulls (EXEMS 60/1985.292 and BRSUG 27200) from the Otter Sandstone Formation, South Devon coast, England, belong to different taxa (*Fodonyx spenceri* and *Bentonyx sidensis*, respectively), neither of which can be safely assigned to the most complete postcranial skeleton collected in the area (EXEMS 79/1992). *F. spenceri*

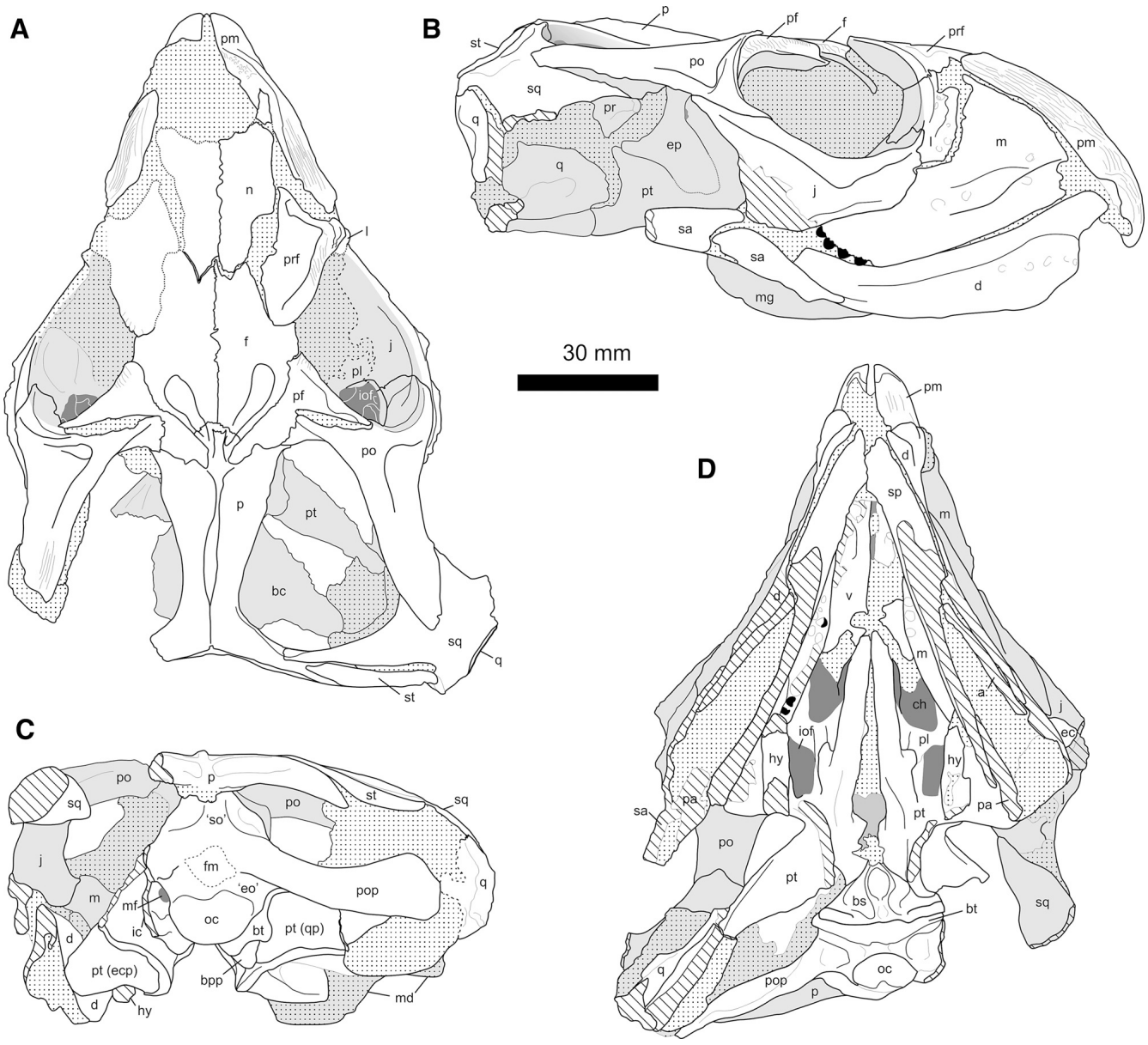

FIGURE 2. Line drawings of the holotype of *Bentonyx sidensis* (BRSUG 27200, partial skull) as preserved. **A**, dorsal; **B** right lateral; **C**, occipital; **D**, ventral views. Hatched and dotted areas represent broken surfaces and sediment cover respectively; worn-out and unworn teeth depicted in white and black, respectively; light gray represent structures on the background and dark gray internal apertures/breakages.

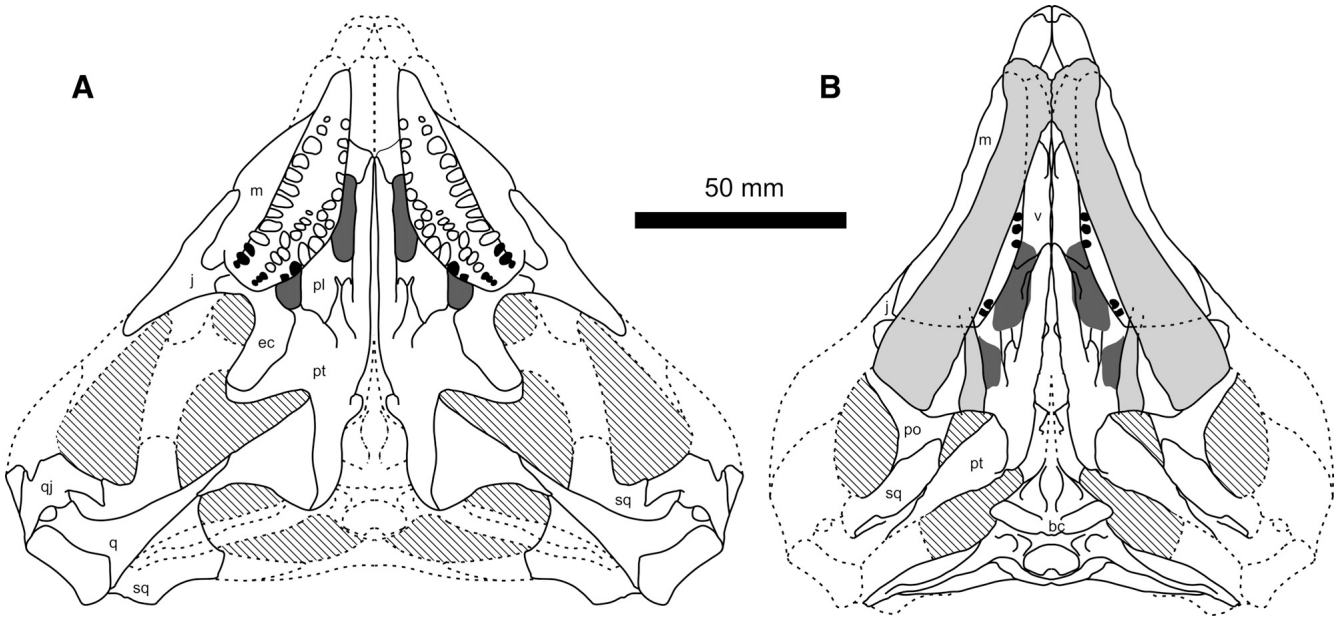

FIGURE 3. Skull shape of the Devon rhynchosaurs, reconstructed (for comparison) in ventral view from the more complete sides and mirrored. **A**, *Fodonyx spenceri* (EXEMS 60/1985.292); based on Benton (1990); **B**, *Bentonyx sidensis* (BRSUG 27200); mandible and hyoids represented in light gray. Hatched areas represent skull openings and dotted lines reconstructed parts based on one another, as well as on the general rhynchosaur morphology; other conventions as in Figure 2.

represents the sister taxon to the Late Triassic Hyperodapedontinae, whereas *B. sidensis* may have a more basal position within that lineage, or represents the sister taxon to a clade composed of *Stenaulorhynchus stockleyi* and 'Mariante-rhynchosaur.' This strengthens the importance of the rhynchosaur diversity of the Anisian Otter Sandstone Formation, which may include basal members of the two major rhynchosaur radiations, the Middle Triassic south Pangean 'stenaulorhynchines' and the Late Triassic cosmopolitan hyperodapedontines.

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This paper represents a joint effort of most of the very few people presently working with rhynchosaurs in honor of Michael

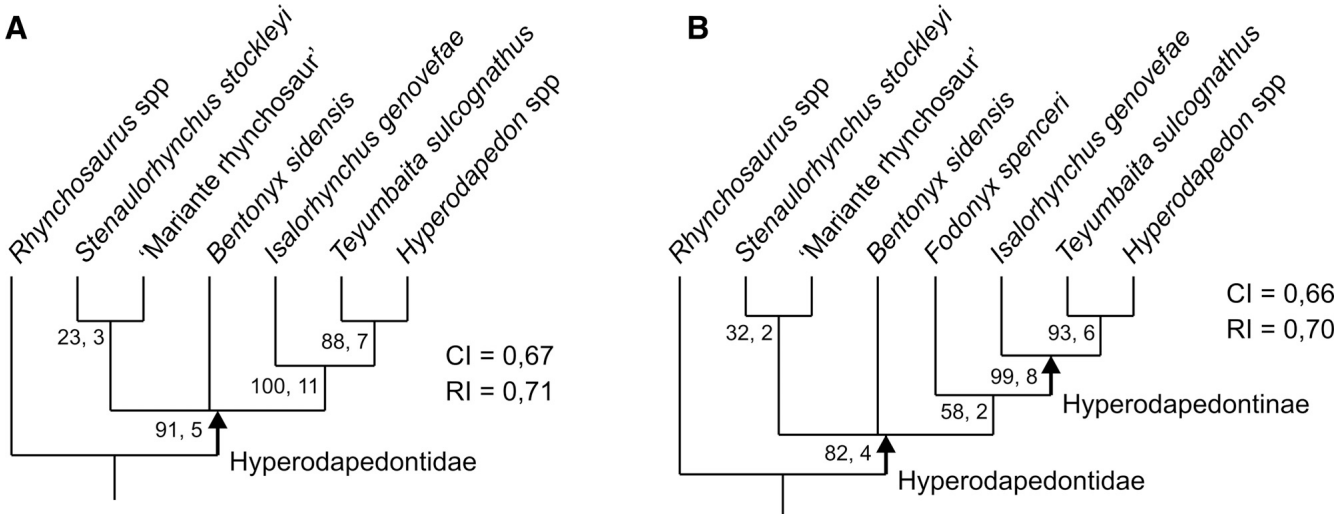

FIGURE 4. Phylogenetic relations of the Rhynchosauridae depicting the positions of the South Devon coast taxa. **A**, strict consensus of the two MPTs recovered in the analysis without *Fodonyx spenceri*; **B**, strict consensus of the two MPTs recovered in the analysis including *F. spenceri*. Bootstrap (1000 replicates) and 'Bremer support' values of each node are indicated. Non-rhynchosaurid rhynchosaurs (*Mesosuchus* and *Howesia*) were pruned from the graphic. Arrows designate stem-based taxa. Characters supporting Hyperodapedontidae: (1) prefrontal with depressed dorso-medial surface; (2) parietal with laterally directed transverse processes; (3) suborbital fenestra bordered only by ectopterygoids and palatines; (4) ilium with cranial process longer than 15% of caudal process. Characters supporting Hyperodapedontinae: (1) anguli oris crest reaching the rostral margin of the jugal; (2) ventral process of squamosal broader than 50% of its dorsoventral length; (3) mandible deeper than 25% of its total length; (4) maxilla with 'pyramidal' teeth. **Abbreviations**: **CI**, consensus index; **RI**, retention index.

James Benton, probably the most prominent palaeontologist to spend a significant amount of time investigating this reptile group. Mike is responsible for helping the various authors here in their careers and research over the years and this represents a small 'thank you' from us to him. We are indebted to L. Loeffler (BRSUG), M. C. Malabarba (MCP), and R. Martinez (MCNSJ) for allowing study of specimens under their care. Thanks also to M. B. Andrade for additional photographs of BRSUG 27200, and to the JVP editors and reviewer for handling/reviewing the manuscript.

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