

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

MAX C. LANGER,<sup>\*1</sup> FELIPE C. MONTEFELTRO,<sup>1</sup> DAVID E. HONE,<sup>2</sup> ROBIN WHATLEY,<sup>3</sup> and CESAR L. SCHULTZ<sup>4</sup>;  
<sup>1</sup>Laboratório de Paleontologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes 3.900, 14040-220, Ribeirão Preto, São Paulo, Brazil, mclanger@ffclrp.usp.br; feio.bio@yahoo.com.br; <sup>2</sup>Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xiwai Street, 100044, Beijing, China, dwe.hone@yahoo.com; <sup>3</sup>Science and Mathematics Department, Columbia College, 600 S. Michigan Ave., Chicago, Illinois 60605, U.S.A., rwhatley@colum.edu; <sup>4</sup>Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, 91501-970, Porto Alegre, Rio Grande do Sul, Brazil, cesar.schultz@ufrgs.br

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 (‘stenaurohynchines’) 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, basiptyergoid 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, interfenestral 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 PALAEOONTOLOGY

DIAPSIDA Osborn, 1903  
ARCHOSAURIFORMIA 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

\*Corresponding author.