Journal of Vertebrate Paleontology 27(3):709–710, September 2007

SHORT COMMUNICATION

NEW EVIDENCE FOR THE CONTROVERSIAL "LUNGS" OF THE LATE DEVONIAN ANTIARCH *BOTHRIOLEPIS CANADENSIS* (WHITEAVES, 1880) (PLACODERMI: ANTIARCHA)

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The bothriolepidid euantiarch *Bothriolepis canadensis* (Whiteaves, 1880) is known from the Upper Devonian (Frasnian) Escuminac Formation at Miguasha, Quebec, Canada, and has been extensively studied because it is extremely abundant and represented by well preserved articulated specimens (e.g., Stensiö, 1948; Werdelin & Long, 1986; Vezina,1996). In addition, and in common with other fishes from the Konservat-Lagerstätte of Miguasha (Jarvik, 1980; Janvier et al., 2006), it is the only known antiarch that displays some exceptional soft-tissue preservation (Patten, 1904; Denison, 1941, 1978; Arsenault et al., 2004). These are nevertheless limited to imprints of the scale-less trunk, traces of the digestive tract (notably the scrolled spiral intestine and some possible cololites) and imprints of blood vessels against the internal surface of the thoracic armour. Denison (1941) brought to light some of these internal structures by making horizontal, sagittal and transverse sections through five excellent specimens formerly collected by William Patten (Dartmouth College, New Hampshire). He also pointed out a peculiar paired accumulation of very fine-grained sediment in the anterior part of the thoracic armour, ventral to the presumed gill chamber, and which he interpreted as the filling of "lungs," because they had much the same "position and relationships as the lungs of certain dipnoans and tetrapods" (Denison, 1941: 558). This surprising interpretation was variously received. Some were skeptical (Myers, 1942; Stensiö, 1948), whereas others considered it plausible (Romer, 1945, 1968). In the mid twentieth century, the Escuminac Formation was regarded as a lake deposit submitted to periodical drought (Denison, 1941), and this was supposed to explain why its fossil fish fauna comprised so many, presumably air-breathing piscine relatives of the terrestrial vertebrates. Actually, it yields two lungfishes (*Scaumenacia*, *Fleurantia*), which certainly possessed lungs, and other sarcopterygians (the porolepiforms *Holoptychius* and *Quebecius*, and the tetrapodomorph *Eusthenopteron*), which were supposed to have possessed lungs as well. Although placoderms were then regarded as related to chondrichthyans, the presence of lungs in an antiarch living in the same environment was then considered as plausible, as if the entire Miguasha fish fauna showed a general "trend" toward terrestrialization. In addition, most other occurences of *Bothriolepis* worldwide are in terrigenous facies (e.g., the "Old Red Standstone") that were regarded as temporary lake or river deposits. However, the hypothesis of the presence of "lungs" in *Bothriolepis* progressively fell in oblivion; yet it is sometimes resurrected (Wells and Dorr, 1985).

The discovery of soft-tissue preservations of relatively large blood vessels against the internal surface of the anterior ventrolateral plate (AVL) of the thoracic armour of *B. canadensis* gave some credit, if not to the "lung" hypothesis, at any rate to the possibility of the presence of paired pharyngeal diverticles close to the branchial chamber (Arsenault et al., 2004:figs 1–3). These blood vessels apparently radiate from a ventral anteromedian area where the heart is assumed to have been situated in the thoracic armour of placoderms, and expand onto the subcephalic part of the right and left AVL plates. Consequently, these blood vessels occupy approximately the same surface as the "lungs" described by Denison (1941). Nevertheless, the latter considered that these "lungs" could extend farther back, posteriorly to the postbranchial lamina (anterior internal transverse crest), as illustrated in his reconstruction (Denison, 1941:fig.10, 1978:fig. 8) and confirmed by the specimen described below.

A recently discovered specimen of *B. canadensis* from the Escuminac Formation provides the first three-dimensional evidence for the actual presence of large paired masses of fine-grained sediment, in exactly the same position and with an almost similar size as those referred to "lung" fillings by Denison (1941) (Fig. 1). The specimen was split horizontally, but the paired "lung"-like structures remained intact and separated well from the coarser surrounding sediment, because they are coated with a thin dark film that may be a remnant of some soft tissue layer. This film seems to be thicker on the posteroventral surface of the left "lung"-like structure (Fig. 1A, arrowheads) and a large patch of it is conspicuous in the same area on the dorsal counterpart of the specimen. Such dark films that coat presumed soft-tissue preservations in *B. canadensis*, including the imprints of the blood vessels, are generally referred to as "carbonaceous imprints" or "tarry imprints." However, their brownish colour when weathered suggests that they contain in fact a large quantity of pyrite. At the junction between these paired masses of fine-grained sediment, there is a ventrally-placed median structure filled with even finer-grained sediment (Fig. 1B), and which could correspond to what Denison (1941:figs.2, 4) interpreted as the filling of the esophagus.

Although this new specimen corroborates Denison's (1941) long debated description, the significance of these paired masses of fine-grained sediment remains elusive. Their approximate congruence with the extension of a large vascular plexus may still support Denison's suggestion that they are the natural cast of some accessory respiratory organs, yet not necessarily "lungs." However, modern teleosts display a variety of other kinds of pharyngeal and esophagal diverticles, some of which are in-

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