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“Lungs” in Placoderms, a persistent palaeobiological myth related to environmental preconceived interpretations

Le « poumon » des placodermes, un mythe persistant en paléobiologie lié à des préconceptions environnementales

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ABSTRACT

The presence of an aerial breathing organ in Placoderms is noticed in many textbooks on the history of breathing in Vertebrates. The origin of this interpretation is from a paper published in 1941 dealing with the interpretation of the differential sedimentary infilling of the armour of the antiarch *Bothriolepis canadensis* from the Late Devonian Escuminac formation of Canada. A revision of this material shows that if some sedimentary structures could be interpreted as traces of some digestive organs, none could be interpreted as putative lungs. The original proposal was based mainly on a presupposed mode of life of *Bothriolepis* in a freshwater environment of an alluvial plain. Recent studies of the Escuminac Formation environment conclude that it represents a marginal marine environment. Moreover, *Bothriolepis* has a worldwide distribution, notably in strictly marine environment. Thus, the presence of lungs in *Bothriolepis* remains highly questionable: it cannot be supported by anatomical, phylogenetic, nor biological arguments.

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RÉSUMÉ

La présence d'un organe respiratoire aérien chez les Placodermes est mentionnée dans nombre d'ouvrages généraux sur l'histoire de la respiration chez les vertébrés. La source de cette question se trouve dans un article de 1941, consacré à l'interprétation du remplissage sédimentaire de la carapace de l'antiarche *Bothriolepis canadensis* de la formation d'Escuminac. La révision de ce matériel montre que, s'il est possible d'interpréter certains remplissages comme une substitution possible des organes viscéraux digestifs, rien n'indique la présence d'organes pouvant représenter des poumons. L'interprétation proposée à l'époque reposait principalement sur un mode de vie presupposé de l'animal dans un environnement d'eau douce de plaine alluviale. Des études récentes de l'environnement de la formation d'Escuminac concluent à un milieu marin côtier. De plus, le genre

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Bothriolepis a une distribution mondiale, notamment dans de nombreux environnements marins francs. Morphologiquement non vérifiable, la présence de poumons chez *Bothriolepis* n'est soutenable, ni phylogénétiquement, ni biologiquement.

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1. Introduction

In many textbooks and web pages related to the history of air breathing, placoderm fishes are often cited as the earliest vertebrates with both gills and lungs.

Some examples are quite explicit about it. For instance, Liem and al. (2001: 59) stated: "Based on internal molds of the body cavity, some workers have interpreted that *Bothriolepis* had lungs; if so, then lungs evolved independently in antiarchs and osteichthyans based on the distribution of other characters." On page 585, they added "Lungs are one of many aerial respiratory organs to have evolved in fishes. Many bony fishes have either lungs or swim bladder. . . so these organs are a common character of the group. . . lungs appear to have arisen early in evolution. Lungs may have evolved in certain Placoderms and primitive bony fishes that were living in stagnant freshwater habitats subject to periodic droughts during the Late Silurian and Devonian periods".

The idea has been reproduced in well-known encyclopedias for example in the *Encyclopaedia britannica* (2010). In the concise version of this encyclopedia, an article on *Bothriolepis* states:

"...The genus apparently had functional lungs, indicating that lungs are very ancient structures. It is probable that *Bothriolepis* was a bottom-dwelling animal inhabiting streams and lakes and pulled itself about along the bottom with its hooklike arms."

Other example can be taken from the Biology course at the University of Massachusetts (2010): "...Based on internal molds of the body cavity, some workers have interpreted that *Bothriolepis* had lungs; if so, then lungs evolved independently in antiarchs and osteichthyans based on the distribution of other characters".

Claiming the presence of lungs in the antiarch genus leads to paleobiological scenarios which are hardly testable and seem more like paleopoetry than scientific investigation (Murphy, 2006).

This appears clearly in the following statement (museum of the Carleton University, Department of Earth Sciences, 2009): "Serially sectioned specimens of *Bothriolepis* show that inside the armour the fish had paired lung-like organs and a spiral intestine, preserved full of organic sediment differing from the sediment type surrounding the fossil. It was quite probably a mud-grubber that ingested organic-rich mud for its food. Its long pectoral appendages could also have been used to push itself deeper into the mud for feeding. *Bothriolepis* is known mostly from freshwater deposits which they must have invaded through shallow seaways as well as rarer marine sites such as the Devonian reefs at Gogo in Western Australia".

The question of "lungs" in *Bothriolepis* has been revived by two recent papers on new material from the Miguasha Museum of Natural History (Arsenault et al., 2004; Janvier

et al., 2007). Even if the question is presented as controversial, the "evidence" claimed in the title of the second paper needs to be evaluated from the same critical perspective as that expressed in its conclusion. In recent forms, the presence of both operational lungs and gills does exist in lungfish and some indications let us think there was a similar breathing system in fossil coelacanth even if in extant ones, the "lung" has been replaced by a fatty organ (Brito et al., 2010). The impact of the hypothesis of an aerial breathing organ in *Bothriolepis* has been crucial in several other scientific studies concerning the evolutionary history of breathing in vertebrates (Perry et al., 2001). In Roux (2002), the conclusion in terms of phylogenetic distribution is even more explicit: "Il est même possible que la présence d'un organe aérien ventral soit primitive chez l'ensemble des Gnathostomes. En effet, des traces fossiles d'une paire de sacs ventraux reliés par un conduit commun à la jonction œsophagopharyngienne ont été identifiées sur le Placoderme fossile *Bothriolepis canadiensis* (sic). Selon cette hypothèse, les chondrichtyens, représentés à l'heure actuelle surtout par les Elasmobranches (requins, raies. . .), auraient perdu secondairement cet organe aérien ventral" (Roux, 2002).

The original ideas about lungs in Placoderms stem from a paper published in 1941 by Robert H. Denison, then a young researcher who based his work on the abundant material of *Bothriolepis* gathered by William Patten in the Escuminac Bay area of Canada and stored in the Dartmouth College collections. This abundant material contained a number of articulated complete specimens preserved in three dimensions and supposedly fossilized in normal living position. At the beginning of 20th century, Patten (1904, 1912) had already sectioned part of this material transversally and horizontally and remarked that within the infilling of the armor were different sediments, some of them showing striking differences with the outside matrix, as if there were some sort of filtration. Within the body carapace, he distinguished some laminated internal structures that he interpreted on the figure as gills (Patten, 1904, fig. 2; 1912, fig. 261). The same material was studied by Denison (1941), who reinterpreted it as a spiral intestine even if this structure, as already noted by Patten, is not so evenly preserved in most observed specimens. His interpretations of the internal anatomy are summarized in a "classic" figure (Fig. 1).

In order to check the observations by both authors, I have searched for the original material which was supposed to have been transferred from Dartmouth College to the American Museum of Natural History Collections. Actually, this collection contains a number of Patten's original sections but none of the ones studied and figured by Denison in 1941. A small series of other sections with the same preservation as those of AMNH, occurs in the Field Museum fossil fish Collections in Chicago, where Denison

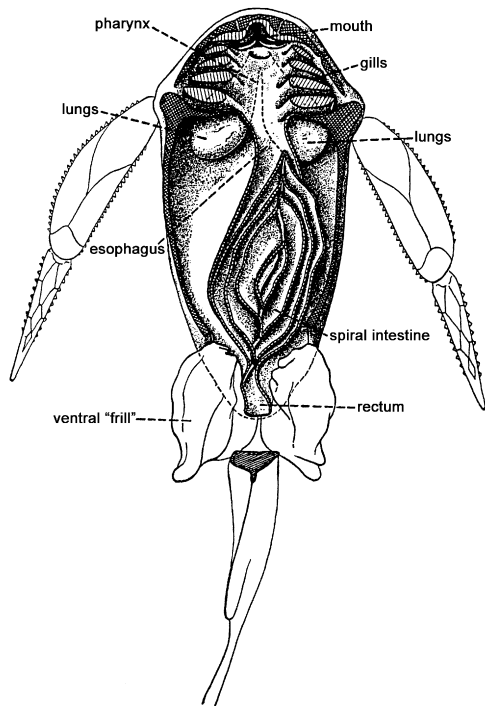


Fig. 1. Denison's reconstruction of the internal soft anatomy of *Bothriolepis canadensis*. The ventral "frill" is a fossilization artefact due to extrusion under pressure of fine sediment from the body armor.

Fig. 1. Reconstitution de l'anatomie des parties molles internes de *Bothriolepis canadensis* selon Denison (1941). La collerette ventrale est un artefact de fossilisation produit par l'extrusion sous pression de sédiment fin, hors de la cuirasse de l'animal.

was curator. As in New York, none of them corresponds to Denison's figures. However the material is clear enough to allow a reinterpretation of Denison's thesis about the soft anatomy of *Bothriolepis* and, as a result, to clarify our views on the structures interpreted as putative "lungs" in Placoderms.

2. List of the examined material

Field Museum of Natural History: specimens PF 3830 (8 sections), PF 3831 (19 sections), PF 3832 (12 sections); all are transverse sections with a thickness of about 5 mm through different individuals with partial head and complete body carapace. Sections had been initially fixed to a glass plate and covered with Canada balsam. Both faces of each section have been examined. In order to determine the original position of the specimen in matrix (i.e. natural or upside down position) other specimens (PF11566, UF 522, UF 54, UF 516, P 25209, PF 6309) have been checked.

American Museum of Natural History: 5 uncatalogued glass plates (reference 38-11 with no specimen number) with glued sections similar to those that have been checked in the Field Museum collection. They do not correspond to the original material recorded by Denison but on two of them a mention of "notochord traces" is written. The author of that mention may be either Denison or Patten. Several

specimens with complete individuals have also been examined in order to determine the taphonomic conditions of fossilization.

3. A revision of Denison's observations

In his paper, Denison interpreted the anatomy of *Bothriolepis* according to the "state of the art" knowledge of his time. On the sagittal section of the head (Fig. 2; Denison, 1941, fig. 9), he represents the various sediments that fill the mouth space. He interpreted as gills a small patch of finer sediment in front of the mouth. In connection with this, the fine sediment continuing backwards is interpreted as the putative "lung" supposed to branch ventrally into the presumed esophagus and extending behind the dermal semilunar plate that delimits the anterior border of the ventral body carapace that extends under the skull. In his global reconstruction of the internal anatomy of *Bothriolepis* (Fig. 1; Denison, 1941, fig. 10), the putative paired "lungs" are located within the body carapace behind the buccobranchial cavity, in the thoraco-abdominal cavity in a way similar to what occurs in terrestrial vertebrates. This reconstruction contradicts our present knowledge of *Bothriolepis* skeletal anatomy (Young, 1984). On his horizontal sections, Denison interprets as "lungs" an irregular patch of fine sediments restricted to the space in front of the anterior transverse crista. This space corresponds to the buccal cavity, which does not extend beyond the anterior internal crista. This crest delimits, on the anterior ventrolateral plate (AVL), ventrally and laterally, the buccobranchial space from the thoraco-abdominal cavity behind it (Fig. 3). It is probable that both cavities were isolated from each other by a membranous separation. The anterior internal crista is the ventral prolongation of the postbranchial lamina (see Stensiö, 1948, fig. 145) that extends on the AVL and more dorsally on the anterior dorsolateral plate (ADL), up to the articular area marking the cervical joint (Fig. 4). There is a contradiction between Denison's observation and

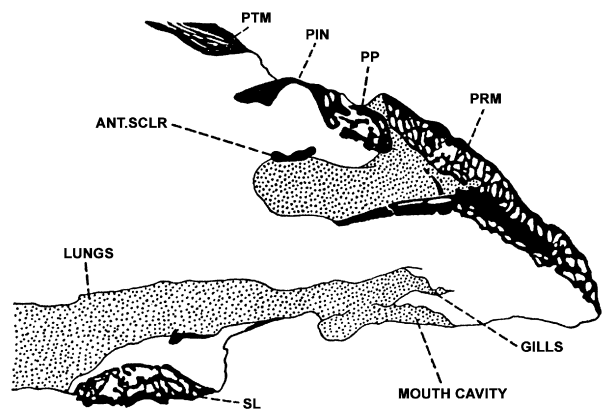


Fig. 2. Sagittal section of the head region of a *Bothriolepis canadensis* from Denison (1941) ANT.SCL: anterior sclerotic plate. PIN: pineal plate. PTM: posttemporal plate. PP: prepineal? plate. PRM: premedian plate. SL: semilunar plate.

Fig. 2. Section sagittale de la tête de *Bothriolepis canadensis* d'après Denison (1941). ANT. SCL: plaque sclérotique antérieure. PIN: plaque pinéale. PTM: plaque postpinéale; PP: plaque prépinéale? PRM: plaque prémédiane.

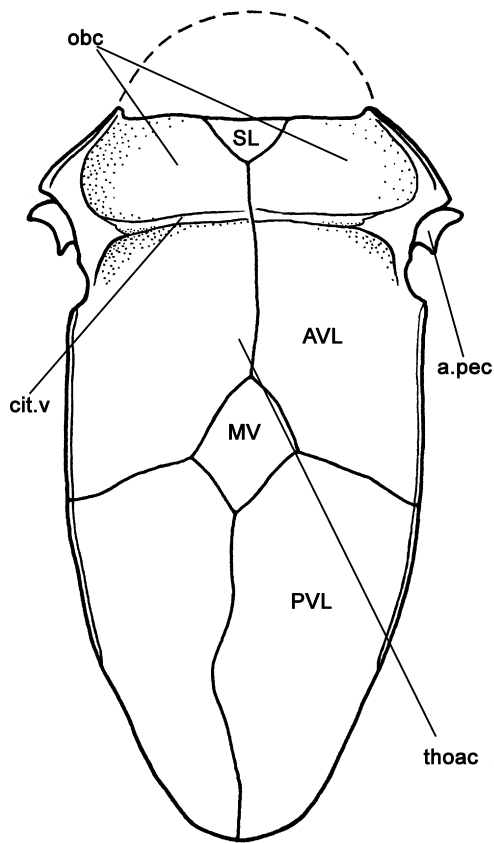


Fig. 3. *Bothriolepis canadensis*: internal view of the body carapace. AVL: anterior ventrolateral plate. MV: median ventral plate. PVL: posterior ventrolateral plate. SL: semilunar plate. a.pec: pectoral fin articulation. cit.v: anterior crista transversalis interior. obc: oralobranchial chamber. thoac: thoraco-abdominal chamber.

Fig. 3. *Bothriolepis canadensis*: vue interne du plastron de la carapace. AVL: plaque ventrolatérale antérieure. MV: plaque médiane ventrale. PVL: plaque ventrolatérale postérieure. SL: plaque semilunaire. a.pec: articulation de la nageoire pectorale. cit.v: crista transversalis interne antérieure. obc: espace oralobranchial. thoac: espace thoraco-abdominal.

his reconstruction of a pair of “lungs” within the thoraco-abdominal space.

In a recent study of vascular traces exceptionally preserved in some Miguasha *Bothriolepis* specimens, Arsenault et al. (2004) did remark that some of the vascular traces present on the internal surface of the anterior lamina of the AVL plates could be interpreted as the irrigation of the putative “lungs”. Then, according to the distribution of blood vessels, these organs should be placed under the branchial basket, not behind the ventral anterior crista as in Denison’s reconstruction. Given the position of the opercular plate, (named “extralateral plate” in the classic antiarch terminology, Denison, 1978, figs. 88, 90), it is highly improbable that the small space under the branchial basket could be occupied by any large structure that would occupy a good part of the remaining mouth space. Therefore, a “lung” cannot be situated within the oralobranchial space.

Recently, on another specimen, Janvier et al. (2007) described a mass of fine sediment lined by a dark staining expanding into the body armor, slightly behind the

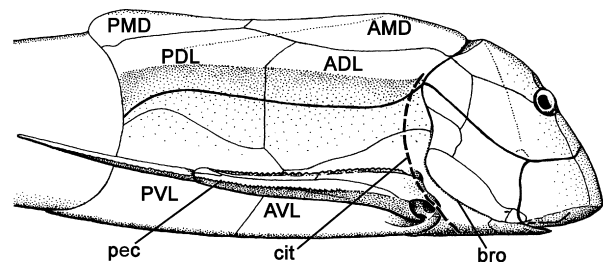


Fig. 4. *Bothriolepis canadensis* lateral view of the carapace from Arsenault et al. (2004) The broken line (cit) follows the lateral and dorsal extension of crista transversalis interna anterior. ADL: anterior dorsolateral plate. AMD: anterior median dorsal plate. AVL: anterior ventrolateral plate. PDL: posterior dorsolateral plate. PMD: posterior median dorsal plate. PVL: posterior ventrolateral plate. bro: branchial opening. cit: crista transversalis interna anterior. pec: pectoral fin.

Fig. 4. *Bothriolepis canadensis* vue latérale de la carapace d’après Arsenault et al. (2004). La ligne en tireté (cit) souligne le tracé latéral et dorsal de la crista transversalis interne antérieure. ADL: plaque dorsolatérale antérieure. AMD: plaque médiane dorsale antérieure. AVL: plaque ventrolatérale antérieure. PDL: plaque dorsolatérale postérieure. PMD: plaque médiane dorsale postérieure. PVL: plaque ventrolatérale postérieure. bro: ouverture branchiale. cit: crista transversalis interne antérieure. pec: nageoire pectorale.

postbranchial lamina. They considered that it could represent the supposed “lungs” or some accessory respiratory organs like the ones hypothesized by Denison (1941). But in that case again, the supposed “lungs” would be a posterior expansion of the oralobranchial chamber. Their analysis, based on a differential infilling of the body carapace, just like Denison’s, adds new arguments in favor of a breathing organ, and the authors, in their conclusion, keep the question open in expressing some doubt about this interpretation.

Given the number of specimens at hand, these infillings needed to be reexamined with a critical approach, and since the taphonomic conditions may have a major impact on the interpretation, these conditions needed to be checked in detail.

From our present knowledge of the internal anatomy of the *Bothriolepis* carapace, some of which was not available to Denison (1941), it is clear that the evidence supporting the position of the “lungs” in this author’s reconstruction (Fig. 1) has to be seriously questioned. In any case, the reasons presented to support such an interpretation need to be reexamined. Namely, are the arguments presented by Denison in favor of the preservation of the soft anatomy of *Bothriolepis* strong enough? Or is it an over-interpretation of the very complex mixture of sediments filling the dead fish armor? Multiple sources of uncertainty are involved in such interpretations of supposed fossilized anatomical soft structures.

3.1. The taphonomic biases

Denison’s (1941) interpretation is exclusively derived from an analysis of the sediments that fill the carapaces and the supposed mode of life and conditions of death of the fish. Even if not directly expressed, this author, following Patten’s observations and remarks (1912, p. 379), describes the animals as if they had been fossilized in their

life position in a channel or a shallow freshwater pool in a floodplain. The infilling of the carapaces is therefore supposed to witness the conditions of death and sedimentation of the fish carcasses. Denison proposes a scenario with a number of conjectures. First, he compares the feeding habit of *Bothriolepis* with that of earthworms (Denison, 1941, p. 554), explaining why he interpreted the distribution of the finest sediment as traces of the alimentary tract. Then, he invokes turbid waters as the secondary infilling with coarser sediment. With the completely articulated specimens grouped on the same stone (for example AMNH 13105, Parent and Cloutier, 1996, fig. 13; see also Patten, 1912, figs. 249, 250, 257), the fossilization in normal position seems like a realistic interpretation. But a major problem is that most of the *Bothriolepis* carcasses are sedimented reversed with their ventral side up (Patten, 1912, p. 370, fig. 257; Parent and Cloutier, 1996, p. 74), and this is also the case in most specimens observed in Chicago and New York. The preservation of three-dimensional specimens is related to the condition of deposition. In the material collected in the Wood Bay sandstone in Spitsbergen, a series of three-dimensional specimens of *Porolepis* (Jarvik, 1972, pl. 6, fig. 1) has been collected. In the field, they were all fixed to a harder sandstone layer. The preserved three-dimensional side lays on a soft fine-grained siltstone and is always fixed to the under side of the hard sandstone bed. On sections, the upper half of the specimen is compressed and sometimes disarticulated, the lower half remains tridimensional with little alteration of the original body curvature. They were all in reversed position, the belly up. Such a situation might also occur in the Canadian material, with the best preserved three-dimensional side being at the bottom.

Therefore, the orientation of the sections figured by Denison remains controversial since there is no indication of the original orientation of the specimen. This is an important element because in most of the figured sections, the finest sediment within the carapace is located just adjacent to the belly carapace and the coarser sediment is deposited above it. This contradicts the normal density rules. On most of the actual sections examined, it is the same situation. During the fossilization process, when the specimen is sedimented and with the sediment compaction, the upper face of the carapace is directly under pressure, the lower part is less affected by this compression process. When the upper face corresponds to the ventral shield, it is broken down and when it is the dorsal shield, the breaks appear along the contact between the median dorsal plates and the dorsolateral plate series. Therefore, the sections figured on Denison's fig. 2 should probably be reversed. Then the distribution of the infilling material follows the normal gravity rules with the finest sediment up. This figure raises another question: Denison figures on the same sections of the supposed esophagus together with the presumed intestine that was supposed to follow it backwards. A close examination of the actual sections also shows that the granulometry distribution in the filling sediment is not as clear as represented in Denison's selected sections. In most of them (AMNH. 38-11, FMNH PF.3832, Fig. 5), the fine sediment is erratically contorted and no precise detail can suggest definite organs within the body armor. It seems that the

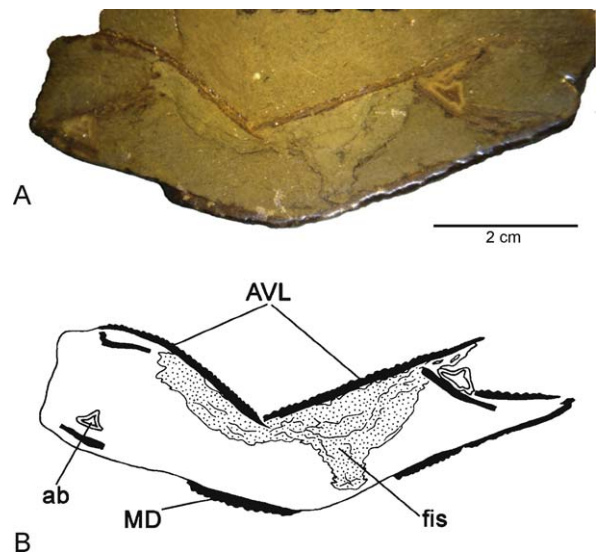


Fig. 5. *Bothriolepis canadensis*, transverse section of the body (FMNH.PF 3832 in fossilization position, the ventral side up, ventro-dorsally compressed). A: Photo of the section. B: Interpretation scheme. AVL: anterior ventrolateral plate. AMD: median dorsal plate. ab: fossilised air bubble. fis: fine infilling contorted sediment.

Fig. 5. *Bothriolepis canadensis*, section transversale du tronc (FMNH.PF 3832 en position de fossilisation, le ventre en l'air, comprimé ventro-dorsalement). A: Photo de la section. B: Schéma interprétatif. AVL: plaque ventrolatérale antérieure. AMD: Plaque médiane dorsale. ab: bulle d'air comprimée et fossilisée. fis: sédiment fin de remplissage.

fine textured sediment penetrated the cavities and filled it during or after decomposition had taken place. There is no reason to suppose that the food tract had been filled by ingestion during the animal life: the “earthworm feeding” comparison is not supported by these data. The maceration inside the armor led to a distribution of the sediment more or less according to the granulometry, with the finer material and the remaining organic matter above the coarser sediment.

This observation had already been done by Patten (1912, p. 378) who remarked that “In (most) cases the viscera (sic) were found either on the dorsal or on the ventral wall of the branchiocephalon (i.e. the bony armor), according to the side that happened to be uppermost when the animal died”. Patten calls “viscera” the fine sediment he supposes had replaced the soft tissue. This is confirmed on sections FMNH PF 3830 (Fig. 6) where, stained with malachite green, a fine laminated sediment rich in organic traces is clearly visible. It corresponds to what was initially interpreted as a trace of spiral intestine by Denison. However, it does not occupy the position it should occupy if the fossilization had occurred as supposed by this author, that is with the animal ingesting the mud. A closer look at the slide shows that the putative intestine is located under the median dorsal plate, marked by the dorsal sensory line. Given the preservation, we are unable to determine if the section of the median dorsal plate corresponds to the anterior or the posterior one, but this is the key element to orient the section. According to the shape of the section, the main pressure operated obliquely on the dorsal side of the carapace and a break is observed at the contact between the median dor-

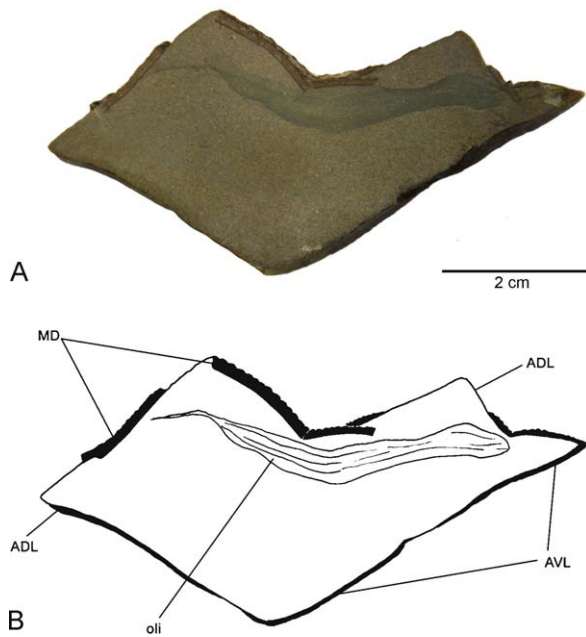


Fig. 6. *Bothriolepis canadensis*, transverse section of the body (FMNH.PF 3830f. in fossilization position, dorsal side up). The compression has crushed the carapace obliquely. A: photo of the section; the grey-blue trace is due to malachite green staining. B: Interpretation of the same section. ADL: anterior dorsolateral plate. AVL: anterior ventrolateral plate. AMD: median dorsal plate. oli: organic laminated infilling (stained with malachite green).

Fig. 6. *Bothriolepis canadensis*, section transversale du corps (FMNH.PF 3830f. en position de fossilisation, le dos en l'air). La compression a écrasé la carapace en oblique. A: photographie de la section; la bande transversale gris-bleu est due à la coloration par du vert de malachite. B: schéma d'interprétation. ADL: plaque dorsolatérale antérieure. AVL: plaque ventrolatérale antérieure. AMD: plaque médiane dorsale. oli: remplissage organique feuilleté (coloré au vert de malachite).

sal plate series and the anterior dorsolateral one. In that case, the so-called “intestine” is just under the dorsal carapace. This confirms the presence of a gradient in the infilling sediment. The finer sediment, with its organic traces, is located above the coarser one and its interpretation as traces of an “intestine” is questionable. It may not represent the internal soft parts. In some other sections (FMNH PF 3832: Fig. 5), the infilling is composed of a core of very fine limy sediment without laminated structures, but with a cloudy erratic distribution of what could be interpreted as remains of organic matter. This central fine sediment is surrounded by coarser one matrix with similar erratic traces of darker material. One can remark also in several places stellar spaces that may represent compressed bubbles released by gaseous decay during the fossilization process.

To conclude, given the information at hand and despite the absence of examination of the original material, the plausibility of the interpretation of soft parts by Denison is highly dependent on the condition of fossilization of the studied material, conditions that remain unclear. It would be necessary to corroborate his observations by sectioning three-dimensional material with specimens that have been properly oriented in situ. Even if some of his observations appear correct, his interpretations were clearly also highly

biased by the ideas available at the time concerning the anatomy and the supposed mode of life of *Bothriolepis*.

4. The environmental interpretation

The most important argument developed by Denison concerns the supposed environment of the Escuminac Formation. Until recently, most of the Devonian turgidous beds with their rich vertebrate faunas were supposed to be from a strictly freshwater environment. This idea led to consider that the original environment for vertebrates was fresh-water and that marine forms appeared later in the Upper Devonian. This idea, proposed by Romer and Grove (1935), dominated the scientific community and remains popular among paleontologists and geologists (Laurin et al., 2007). The important role played by these authors in North America, along with inclusion of these ideas in a popular vertebrate paleontology textbook (Romer, 1966), may explain why these ideas were so widespread and Denison's contribution supported this theory. Considering the geological conditions of the Escuminac Formation and following Patten's observations of the taphonomy of *Bothriolepis* carcasses, Denison concluded that during the fossil deposition there was a constant current under continental conditions, indicating fluvial conditions in a flood plain. Then, he analysed the faunal composition of the Escuminac formation and drew from it arguments in favor of his interpretation of fine sedimentary “pharyngeal pouches” as putative lungs. Denison wrote (1941 p 558): “That this Upper Devonian fish should possess lungs as well as gills is not as remarkable as it might seem at first sight. It is known that Amphibia had appeared by Upper Devonian times and presumably possessed functional lungs derived from those of the crossopterygian ancestors. Two crossopterygians, *Eusthenopteron* and *Holoptychius* are found in the same beds as *Bothriolepis*. The “lung-fish” or dipnoan *Scaumenacia* is another element of the same fauna and it is very possible that it had already developed lungs. . . . Finally the geological sequence indicates fluvial conditions (. . .) these are precisely the conditions under which could occur occasional droughts and presumably those under which lungs originated”.

Two of the arguments developed by Denison have presently been refuted: first, the phylogenetic analyses have concluded that lungs are an apomorphy of Osteichthyans (Graham, 1997). The “necessity” to develop lungs in *Bothriolepis* is a typical “ad hoc” solution which is not devoid of circular reasoning. Second, the environmental interpretations of the Escuminac Formation have been revised, and from its faunal composition (Schultze and Cloutier, 1994) as well as its geochemistry (Chidiac, 1994), it is now established that it represents a marginal marine environment. At the time when Denison wrote his paper, *Bothriolepis* was considered to be a fresh water indicator. More recently, *Bothriolepis* has been found in several strictly marine environments: in Australia (Gogo: Young, 1984; Long and Trinajstic, 2010), USA (Nevada: Schultze, 2010) as well as in marginal marine ones (Miguasha: Schultze and Cloutier, 1994). Moreover, this genus has a worldwide distribution (Young, 1990), which cannot be explained for a freshwater form. So, if the freshwater

environment had been used as an explanation for the development of “lungs” as argued by Denison, the preceding facts can be used as a refutation of the mandatory presence of lungs in *Bothriolepis*.

5. Conclusion

The presence of “lungs” in *Bothriolepis* is an interpretation that reflects general ideas developed during the mid 20th century about the origin of the terrestrial adaptation to life on land. *Bothriolepis canadensis* was supposed to live in fresh water and in seasonally arid land, like the tetrapodomorph *Eusthenopteron*. We now know that the locality in which it was preserved represents a marginal marine environment and no evidence of seasonal drought remains (Laurin et al., 2007). The anatomical knowledge of *Bothriolepis* does not show any clear evidence of lungs. The interpretation of the postmortem infilling of the animal armor allows in some specimens an interpretation of a possible complex intestine but the putative lungs reconstructed by Denison are based on over-interpretation of the data. Moreover, the lungs cannot be placed where Denison placed them. In the Escuminac Formation, the placoderm group that includes *Bothriolepis* (the antiarchs) is a major component of the fauna in number of individuals (several thousand specimens). An important contribution that had a major influence in the environmental interpretation of the Canadian formation during the mid 20th century was the paper by Romer and Grove (1935) in which they compared pre-Carboniferous agnathans and fishes in order to prove that the original environment for the vertebrates was fresh water. It is nowadays admitted that the reverse is more plausible. Given the recent studies of the Escuminac Formation and the worldwide distribution of *Bothriolepis* in very different types of sedimentary and faunal environments, it is now reasonable to consider a possible marine coastal dispersion as more reasonable than a fresh water origin.

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