A new phlegethontiid specimen (Lepospondyli, Aistopoda) from the Late Carboniferous of Montceau-les-Mines (Saône-et-Loire, France)

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ABSTRACT

A new specimen of aistopod from the famous Stephanian deposits of Montceau-les-Mines was discovered in the collections of the Muséum d'Histoire naturelle d'Autun. It is the first nodule of this site that has been studied by X-ray tomography. This specimen is probably a juvenile of the genus *Phlegethontia*, also known in the Westphalian of North America and eastern Europe. The teeth of this animal seem pedicellate, which would reveal that this character was more homoplasic than previously suggested. It also seems that aistopods were terrestrial rather than aquatic.

KEY WORDS
Amphibia,
Lepospondyli,
Aistopoda,
Phlegethontia,
Montceau-les-Mines,
CT-Scan,
pedicellate teeth.

RÉSUMÉ

Un nouveau spécimen de phlegethontiide (Lepospondyli, Aistopoda) du Carbonifère supérieur de Montceau-les-Mines (Saône-et-Loire, France).

Un nouveau spécimen d'aïstopode provenant du fameux gisement stéphanien de Montceau-les-Mines a été découvert dans les collections du Muséum d'Histoire naturelle d'Autun. Il s'agit du premier nodule de ce gisement à avoir été étudié grâce à la technique de tomographie à rayons X. Ce spécimen est probablement un juvénile attribué à *Phlegethontia*, genre également connu dans le Westphalien d'Amérique du Nord et d'Europe de l'Est. Les dents de cet animal semblent pédicellées, ce qui montrerait que ce caractère était bien plus homoplasique que précédemment suggéré. Il semblerait également que les aïstopodes aient été des animaux terrestres plutôt qu'aquatiques.

MOTS CLÉS
Amphibia,
Lepospondyli,
Aistopoda,
Phlegethontia,
Montceau-les-Mines,
CT-Scan,
dents pédicellées.

INTRODUCTION

Aistopods are Paleozoic limbless amphibians that lived in North America and Europe from the Mid-Visean (Carboniferous) to the Lower Permian (Carroll *et al.* 1998). Some specimens found in France have been mentioned by Thévenin (1910) and Dutuit & Heyler (1994), but they have never been named or described, perhaps because of their poor preservation, which hampered detailed description and production of a comparative diagnosis. For example, a specimen from Montceau-les-Mines (S. 5383) was described by Heyler (1980) but the skull is missing. Dutuit & Heyler (1994) stated that this specimen seemed close to the Bohemian species *Phlegethontia longissima* (Fritsch, 1875) but could not offer a more precise identification because of a lack of diagnostic features. A new specimen (MNHN-SOT-II 101076) has been recently discovered in the "Montceau-les-Mines" collections of the MNHN housed in the Muséum d'Histoire naturelle d'Autun (Saône-et-Loire, France). This specimen comes from the Stephanian B of Montceau-les-Mines (Northern Massif Central), one of the most prolific Lagerstätten from the end of the Paleozoic in Europe which has yielded hundreds of thousands nodules (Chabard & Poplin 1999). The material, consisting of a very small aistopod (skull length = 3.5 mm), may be a juvenile because adults usually reach a skull length of 19.8 mm (Anderson 2002). The skull is preserved in lateral view. Thus, it is the first aistopod from France to be studied in detail even if its preservation does not allow any specific identification. It is also the first nodule of Montceau-les-Mines to be analysed by X-ray computed tomography.

One striking feature of this specimen is the possible presence of pedicellate teeth. This dentition is characteristic of lissamphibians and some dissorophoid temnospondyls, and is thought by some authors (Parsons & Williams 1962, 1963; Bolt 1969, 1979) to be a synapomorphy of a clade including dissorophoids and lissamphibians. The presence of such pedicellate teeth among aistopods would make this character homoplasic among tetrapods.

ABBREVIATIONS

FMNH	Field Museum of Natural History, Chicago;
MNHN	Muséum national d'Histoire naturelle, Paris;
ERM	société Études Recherche Matériaux, Poitiers.

MATERIAL AND METHODS

The nodule MNHN-SOT-II 101076 of "Montceau-les-Mines" collections of the MNHN housed in the Muséum d'Histoire naturelle d'Autun has been broken into four parts. Each block contains the following elements:

- 101076a: skull in left lateral view, dorsal vertebrae, caudal (?) vertebrae;
- 101076b: skull in right lateral view;
- 101076c: dorsal vertebrae;
- 101076d: caudal (?) vertebrae.

The block 101076b was observed through a binocular microscope and prepared for a Scanning Electron Microscopy (SEM) examination.

The specimen was too small and too poorly preserved to allow a mechanical or chemical preparation without damage. Thus, the main part of the block 101076a has been analysed in X-ray computed tomography (CT-Scan). Microtomographic record was performed at the University of Poitiers, France, with a X8050-16 Viscom model.

The specimen was scanned by A. Mazurier (ERM) according to the following parameters:

- energy: 130 kV;
- intensity: 150 µA;
- gain of the camera: 76%;
- integration number: 16;
- zoom of the camera: mode 1;
- projections: 1800/360°, i.e 1/0.2°.

A ring artefacts correction has been done on the original generated µCT slices.

The 1004 final 8 bits-tif format sections of 1004 × 1004 pixels have a resolution and interval of 12.0052 µm (cubic voxel). This is the finest possible resolution, scanning a larger part of the block would have reduced the resolution.

Volume rendering was managed on Mimics 10.11, on each two-dimensional slide, structures of interest were selected with threshold selection and the three-dimensional reconstruction was obtained automatically, by compiling all two-dimensional structures on each slide.

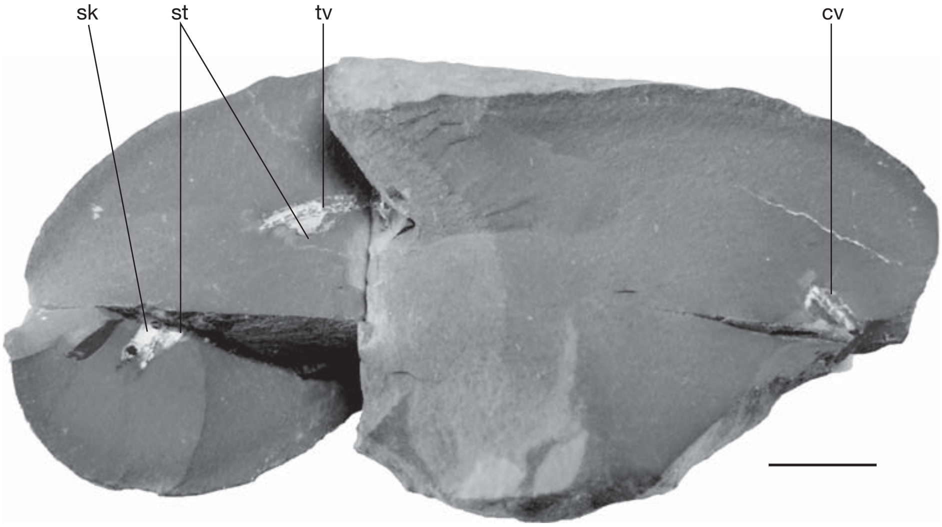

FIG. 1. — Phosphateous nodule MNHN-SOT-II-101076a from the Stephanian B (Upper Carboniferous) of Montceau-les-Mines, France, containing the aistopod *Phlegethontia* sp. as preserved, in lateral left view. Abbreviations: **cv**, caudal vertebrae; **sk**, skull; **st**, soft tissues; **tv**, trunk vertebrae. Scale bar: 1 cm

The anatomical comparisons are made with the Phlegethontiidae *Phlegethontia* in Anderson (2002, 2007), the Pseudophlegethontiidae *Pseudophlegethontia* (Anderson 2003a), the ophiderpetontids *Coloraderpeton* and *Oestocephalus* (Anderson 2003b), and the Lethiscidae *Lethiscus* (Wellstead 1982; Anderson *et al.* 2003). The following description relies overall of an interpretation based on the skull anatomy of *Phlegethontia* rather than an unambiguous identification of individual bones which are difficult to observe on the specimen.

SYSTEMATIC PALEONTOLOGY

Tetrapoda Haywood, 1825
Lepospondyli Zittel, 1888
Aistopoda Miall, 1875
Phlegethontiidae Cope, 1875
Genus *Phlegethontia* Cope, 1871

Phlegethontia sp.

LOCALITY. — "Découverte" (open coal mine) of Saint-Louis, basin of Montceau-les-Mines, Saône-et-Loire, France.

AGE. — Upper Carboniferous (Stephanian B) corresponding to the end of the Kasimovian stage, approximately 303.9 Ma (Gradstein *et al.* 2004).

PRESERVATION

This specimen was discovered in a phosphateous nodule of approximately 6 cm long (Fig. 1). Few parts of the animal are visible. Only the skull and two portions of the vertebral column are distinguishable. The outlines of the animal are visible but do not reveal much detail about the anatomy of soft tissues. At the level of the trunk, the total body height is 3.2 mm, the ventral soft tissues are 1.8 mm high and the dorsal ones 0.3 mm. The main part of the animal remains inside the nodule. Under the SEM, the bones are not distinctly imaged and their sutures are not distinguishable.

The skull is 3.62 mm long in lateral view, with the mouth opened.

The orbit, the external naris, some jaw and mandible bones, and teeth are exposed at the surface of the nodule, the rest of the skull being inside. The skull is broken and fractured near the left side of the animal, and the vertebrae are entire but, again, still inside the nodule.

The X-ray tomography revealed that the specimen was preserved in three dimensions. The block 101076a contains almost all the animal, the skull is nearly complete but it lacks the left mandible and most its left side that might be in the block 101076b. Due to the small size of the specimen and despite the good definition, only the global morphology of the specimen (skull and vertebrae) can be estimated. Finer anatomical details like tooth structure and bone sutures cannot be observed.

DESCRIPTION

Skull (Fig. 2)

The skull is as small as that of the smallest known aistopod (FMNH 831, Anderson 2002: fig. 6). It may be a juvenile individual because adults of *Phlegethontia* may reach a skull length of 19.8 mm (Anderson 2002). The left eye is represented by a black circular mark. Some teeth exhibit two fractures at their base and may be pedicellate (this aspect will be discussed later).

The snout is composed of the premaxilla and is pointed, as is the case in *Phlegethontia* and *Pseudophlegethontia* Anderson, 2003b. The Lethiscidae Wellstead, 1982 and the Ophiderpetontidae Schwartz, 1908 have a more rounded snout, a primitive feature among aistopods (Wellstead 1982; Anderson 2003b). The premaxilla has a posteromesial nasal ramus, and a ventrolateral ramus which bears at least two teeth. A third tooth may be present anteriorly, but remains difficult to observe. The nasal could contact the nasal ramus of the premaxilla. The prefrontal, triangular in shape, contacts the nasal anteriorly and the maxilla or a small lacrimal ventrally. No posterior suture can be observed between the frontal and the postfrontal. The external naris is bordered by the premaxilla, the nasal, the prefrontal, the maxilla and perhaps the lacrimal (Fig. 2). The maxilla looks triradiate. A dorsal and slender bony branch contacts dorsally the ventral branch of the prefrontal. This dorsal branch either belongs to the maxilla or represents a small lacrimal. According to Anderson (2002), the lacrimal disappeared in *Phlegethontia*, remains unknown in *Pseudophlegethontia* because the anterior portion of the skull roof is not preserved (Anderson 2003a), but is retained among the Lethiscidae and the Ophiderpetontidae (Wellstead 1982; Anderson 2003b).

Posteriorly to the premaxilla, a small bar may represent a fragment of the jugal. On the 3D reconstruction, a triradiate shape lies posteriorly to the right orbit and may be the squamosal. One branch is oriented anteriorly, another one posterodorsally and the third one ventrally which bears the quadrate on its extremity.

Within the posterior portion of the orbit, at least six slender ossifications are visible: they are antero-posteriorly elongated, slightly curved and do not show parallel margins. They are comparable with the palpebral ossifications described in some specimens of *Phlegethontia longissima* by Anderson (2002), but never observed in other aistopods (Wellstead 1982; Anderson 2002, 2003a, b). In the studied specimen, the orbit is surrounded by the prefrontal, the maxilla, the jugal, the palpebral ossifications, and perhaps the lacrimal. Other bones that probably bordered the orbit, such as the frontal and the postfrontal are not preserved. In *Lethiscus*, the orbit is borded by the maxilla, the lacrimal, the prefrontal, the postfrontal, the postorbital, and the jugal (Wellstead 1982). The postorbital is absent in Ophiderpetontidae (Anderson 2003b), and is determinable neither in *Pseudophlegethontia* (Anderson 2003a) nor in *Phlegethontia* where, in this last genus, the orbit is bordered by the maxilla, the prefrontal, the frontal, the postfrontal, and the jugal (Anderson 2002). The outlines of the neurocranium are here visible. The dorsal surface is flat, and on the occipital surface, a concave depression forms a notch in lateral view. Posteriorly to the neurocranium, an oblique bar could be the nuchal crest, and a dorsal bar could be the sagittal crest. These crests have only been described in *Phlegethontia* (Anderson 2002). In *Phlegethontia longissima*, the nuchal crest is oriented vertically whereas in the present specimen, it is oriented posteroventrally. The extension of the sagittal crest is difficult to determine but it seems to begin at the same level as the quadrate and reach the posterior limit of the skull.

Mandible

The mandible is poorly preserved, but outlines of dermal tissues can be distinguished. These tissues encompass the mandible with a width of about 30 µm

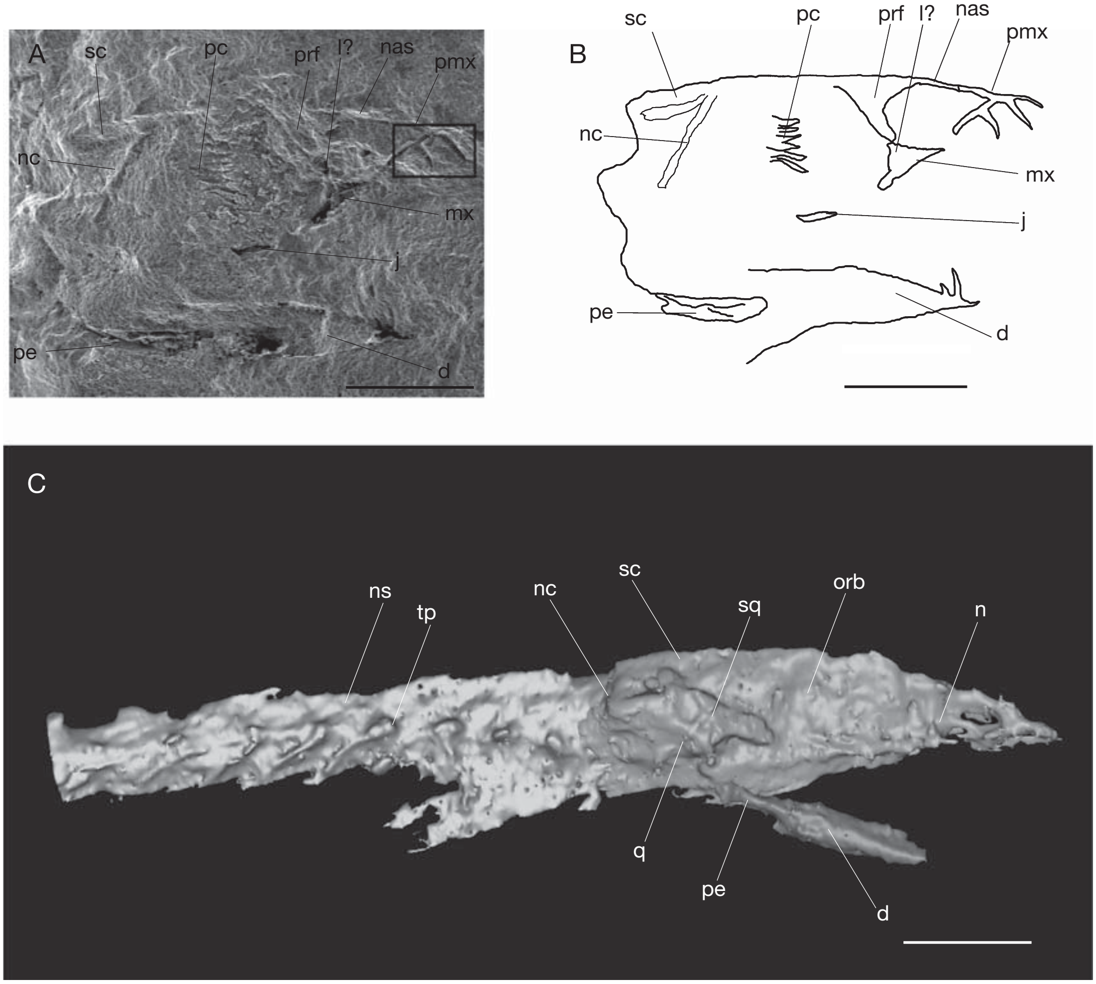

FIG. 2. — Right lateral view of the skeleton of *Phlegethontia* sp. (MNHN-SOT-II-101076b) from the Stephanian B (Upper Carboniferous) of Montceau-les-Mines, France: **A**, SEM photograph of the skull as preserved; **B**, interpretative drawing; **C**, 3D reconstruction of the head and the eight first vertebrae. The frame in A corresponds to the enlarged portion in Figure 3A. Abbreviations: **d**, dentary; **j**, jugal; **l**, lacrimal; **mx**, maxilla; **n**, naris; **nas**, nasal; **nc**, nuchal crest; **ns**, neural spine; **orb**, orbit; **pc**, palpebral cups; **pe**, posterior element of the mandible; **pmx**, premaxilla; **prf**, prefrontal; **q**, quadrate; **sc**, sagittal crest; **sq**, squamosal; **tp**, transverse process. Scale bars: 100 µm.

above the bone, and up to more than 100 µm in the posterior region of the throat. The anterior part of the dentary is present and bears two teeth. In the posterior portion of the mandible, a single straight ossification, ending by an articular condyle, could be the "posterior element", also present in *Phlegethontia* (McGinnis 1967; Anderson 2002). This element may result from the fusion of the articular, the surangular, and the angular which remain discrete in other genera (Anderson 2003a, b; Anderson *et al.* 2003). It articulates on the quadrate condyle that is observable on the X-ray tomography.

Dentition

The teeth seem to be monocuspid, pointed, and slightly curved posteriorly (Fig. 3). They have a maximal length of 0.33 mm for a width of 75 µm at their base. Each preserved premaxilla tooth

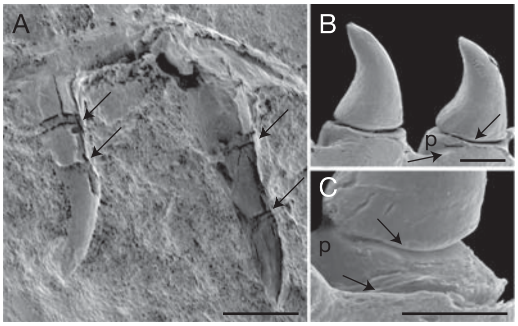

FIG. 3. — Detailed SEM views of: **A**, the anterior part of the upper jaw showing possible pedicellate teeth of *Phlegethontia* sp. (MNHN-SOT-II-101076b) from the Stephanian B (Upper Carboniferous) of Montceau-les-Mines, France; **B**, **C**, pedicellate teeth of the extant urodele *Desmognathus monticola* Dunn, 1916. Arrows indicate zones of weakness. Abbreviation: **p**, pedicel. Scale bars: 100 µm.

surprisingly shows two transverse, slender fractures around its base. One is just above the premaxilla (50 µm) and the other one is distant of 57 µm from the first one. These fractures do not extend into the sedimentary matrix around the teeth, and are therefore interpreted here as natural fractures rather than a post-mortem damage. A natural fracture occurs at the level of a weakness zone, like a pedicellar zone. In *Desmognathus monticola* Dunn, 1916, the pedicels are clearly visible at the base of the teeth, as is the case in most of the other extant urodeles (except sirenids, see Pough *et al.* 2004): each pedicel lies at the base of the tooth, and forms a ring that surrounds the tooth. This decreasing diameter creates a first zone of weakness; a second weakness zone is also visible at the contact between the tooth and the mandible. These pedicels weaken the teeth. The natural fractures observed on the studied specimen, around the base of its premaxillary teeth, could be therefore the result of pedicels. However, pending discoveries of more material of better preservation, the presence of pedicely among aistopods remains uncertain.

Vertebrae

The vertebrae are poorly preserved. On the nodule portions 101076a and c, seven to eight trunk vertebrae of 1 mm long and 0.5 mm high are visible whereas those observed on the posterior part of 101076a and d could be caudal vertebrae, but they are too poorly preserved to allow a better determination.

The X-ray tomography reveals more details on the first eight vertebrae in the block 101076a, even if the preservation and the resolution of such a small specimen does not allow precise observations. The vertebrae cannot be individualized with this method but the transverse processes are visible on the right side of the animal, and extend laterally from the top of the centrum (Fig. 2C). The centrum seems cylindrical and moderately laterally flattened. The height of the neural spine is low, as is the case in *Phlegethontia longissima* rather than in *P. linearis*.

DISCUSSION

TAXONOMIC ATTRIBUTION OF THE JUVENILE AISTOPOD OF MONTCEAU-LES-MINES

Given the poor preservation of the specimen studied here, it is difficult to assign it at the species level. However, the following characters observed on the specimen are typical of *Phlegethontia* (according to the genus definition of Anderson 2002): a pointed snout, presence of sagittal and nuchal crests, of a posterior element of the mandible and of the palpebral cups. These warrant assigning the specimen MNHN-SOT-II-101076 to *Phlegethontia* sp. This would be the second occurrence of this genus in Europe after that of Bohemia. Dutuit & Heyler (1994) already proposed that another aistopod specimen of Montceau-les-Mines (S. 5383), whose skull is unknown, was close to the Bohemian species *Phlegethontia longissima*, Anderson (2002) confirmed this interpretation on the basis of vertebral morphology and the new specimen therefore confirms the presence of this genus in the faunal assemblage of Montceau-les-Mines. All other *Phlegethontia* specimens date from the Westphalian and are thus older that the specimen from Montceau-les-Mines, the only geologically younger Phlegethontiidae Cope, 1875 is *Sillerpeton* Lund, 1978 from Fort Sill (Sakmarian/Artinskian, Lower Permian; Carroll *et al.* 1998).

The specimen has also been included in the matrix of Anderson *et al.* (2003) to which two characters were added (Appendix) and, in spite of the numerous characters that could not be coded in the specimen described above, only four shortest trees of 50 steps have been found and the strict consensus is well resolved (Figure 4 and its caption for the analysis). The studied specimen is in polytomy with both *Phlegethontia longissima* and *P. linearis*. The low number of observable characters on the studied specimen is probably responsible of this low resolution but confirms the hypothesis that this specimen is closely related to *Phlegethontia*. However, no diagnostic character can separate the Montcellian aistopod from the others. Moreover, this specimen is juvenile and may exhibit characters that are not present in adults, and it is too poorly preserved to yield detailed data of the braincase, which are significant in aistopod taxonomy. Another problem is that *Sillerpeton*, which is also incompletly known, cannot be included in phylogenetic analyses because it would add numerous missing data, increase the number of possible trees and reduce the resolution of the consensus. Thus, its relationships with other phlegethontiids remain unknown. It is impossible to assess if the specimen MNHN-SOT-II-101076 is more closely related to *Sillerpeton* or *Phlegethontia* because no characters can be compared between this specimen and *Sillerpeton*.

DID AISTOPODS HAVE PEDICELLATE TEETH?

The possible pedicellate teeth observed in the studied specimen are surprising: nowadays, lissamphibians exhibit this kind of teeth (although they are absent in sirenids and pipids [Pough *et al.* 2004]) and a similar feature is observed in some teleosts (Sire *et al.* 2002; Davit-Beal *et al.* 2007). This character, very rarely reported in Paleozoic taxa, is only found in four dissorophoid genera (*Doleserpeton* Bolt, 1974; *Amphibamus* Cope, 1865; *Tersomius* Case, 1910; *Apateon* Von Meyer, 1844; see Bolt 1969, 1977, 1979; Schoch & Carroll 2003, respectively), and has therefore been interpreted as a synapomorphy relating lissamphibians to dissorophoid temnospondyls (Ruta *et al.* 2003; Schoch & Carroll 2003; Ruta & Coates 2007). However, the pedicely of *Apateon* has been questionned (Schoch & Fröbisch 2006) because on the specimen figured by Schoch & Carroll (2003: fig. 4b), these teeth are broken teeth rather than pedicellate ones (R. Schoch pers. comm.), thus

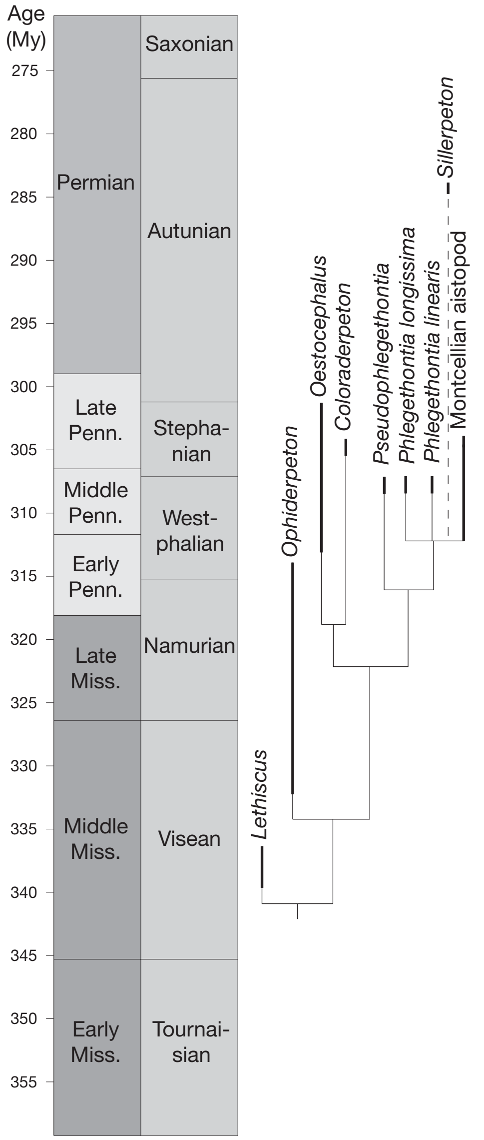

FIG. 4. — Strict consensus of four shortest trees (L = 50 steps, RI = 0.78, CI = 0.68) showing hypothesis of aistopod relationships and placement of the specimen MNHN-SOT-II-101076 (referred as "Montcellian aistopod" on the tree), according to a modified version of the matrix of Anderson *et al.* (2003) augmented with two new characters. The analysis was performed by PAUP*4.0b10 (Swofford 2003), with a branch-and-bound algorithm. The tree has been mapped on a stratigraphic timescale (Gradstein *et al.* 2004). *Sillerpeton* is shown even though it was not included in the analysis. It has been placed close to other Phlegethontiidae (Anderson 2002) but its exact placement is unknown. Abbreviations: **Miss.**, Mississippian; **Penn.**, Pennsylvanian.

pedicely may have evolved only in amphibamids (Schoch 2002; Schoch & Milner 2004; Schoch & Rubidge 2005). Based on this shared presence of pedicellate teeth, dissorophoids (especially amphibamids) are indeed often considered the sister-group, stem-group or even ancestors of all the lissamphibians, or at least of anurans and urodeles (Bolt 1969; Schoch & Carroll 2003; Carroll 2007). Other characters, such as the large interpterygoid vacuities and bicuspid teeth, have been proposed to support this temnospondyl-lissamphibian clade, but they are also found among lepospondyls (large interpterygoid vacuities in some nectrideans and bicuspid teeth in some microsaurs, even in the orientation of the cuspules are different), a group which is therefore also candidate for the origin of lissamphibians (Laurin 1998; Laurin & Reisz 1999; Vallin & Laurin 2004). The possible presence of pedicellate teeth in aistopods suggests that this character could not be considered as an unambiguous synapomorphy supporting a temnospondyl origin of lissamphibians. In consequence, this character may have appeared several times (Fig. 5), once in amphibamid temnospondyls (homologous with lissamphibian pedicely under the temnospondyl hypothesis on the lissamphibian origin) and possibly once in branchiosaurids and in lepospondyls. It has also appeared in some teleosts (Sire *et al.* 2002; Davit-Béal *et al.* 2007) and has been lost in several lissamphibians (Pough *et al.* 2004). Thus, the evolution of this character is much more complex than previously suggested.

However, it is also noteworthy that the lepospondyl origin of lissamphibians is supported by loss features and some homoplasic synapomorphies. Although no phylogenetic analysis suggests a close relationship between aistopods and lissamphibians yet, the presence of pedicellate teeth among lepospondyls would still darken the problem of the lissamphibian origin. But this lightens the principal obstacles to these phylogenetical studies: the extensive homoplasic characters that reign among Paleozoic tetrapods, the large morphological disparity between Paleozoic stegocephalians and lissamphibians, and the huge gap of fossils exhibiting transitory features that could give more precise data about the evolution of characters still unique within lissamphibians. Finally, even if observations made on this juvenile aistopod of Montceau-les-Mines yield only equivocal data about pedicely in this group, it raises the possibility that closer examination of other aistopod specimens would show pedicely to be more taxonomically widespread than currently believed.

TERRESTRIAL AISTOPODS?

Anderson (2002) suggested that *Phlegethontia* led a semi-fossorial lifestyle, in the leaf litter around swamps. He noticed the absence of grooves of the lateral line system on its skull, its rare occurrence in the aquatic deposits of Linton and Nýřany. The same remarks can be made about the lepospondyls of the French Massif Central. *Sauravus* Thévenin, 1906 is a scincosaurid represented by two species: *S. cambrayi* Thévenin, 1910 and *S. costei* Thévenin, 1906 are known from a single specimen and *Scincosaurus spinosus* Civet, 1982 by at least five well-preserved specimens (Dutuit & Heyler 1994). Milner interpreted the presence of few scincosaurids in Stephano-Permian French sites as "terrestrial exotics in the predominantly aquatic faunal assemblages" (Milner 1993: 182). The same remark could be made about aistopods. *Montcellia longicaudata* (Langiaux, Parriat & Sotty, 1974) is an urocordylid known by a unique specimen (Dutuit & Heyler 1994; Steyer *et al.* 1998). In contrast, hundreds of branchiosaurs have been found in the Stephanian of Montceau-les-Mines (Heyler 1994): they are considered as totally aquatic because of their external gills which are sometimes extremely well preserved in the nodules (Heyler 1994). On the other hand, aistopods are extremely rare in the French Carboniferous localities, as in all the other Carboniferous-Permian localities in the world. For example, Milner (1980) counted that in Nýřany, 120 dissorophoid specimens, eight phlegethontiid individuals and 25 ophiderpetondids had been found. According to him, *Phlegethontia* was terrestrial, following the conclusions of Lund (1978) but the other aistopod of Nýřany, *Ophiderpeton* Huxley, 1866, is thought to have been more aquatic.

This probably indicates that some lepospondyls were terrestrial rather than aquatic, such as *Phlegethontia* and *Sauravus* (from the Stephanian of Montceau-les-Mines and Autun). Urocordylids,

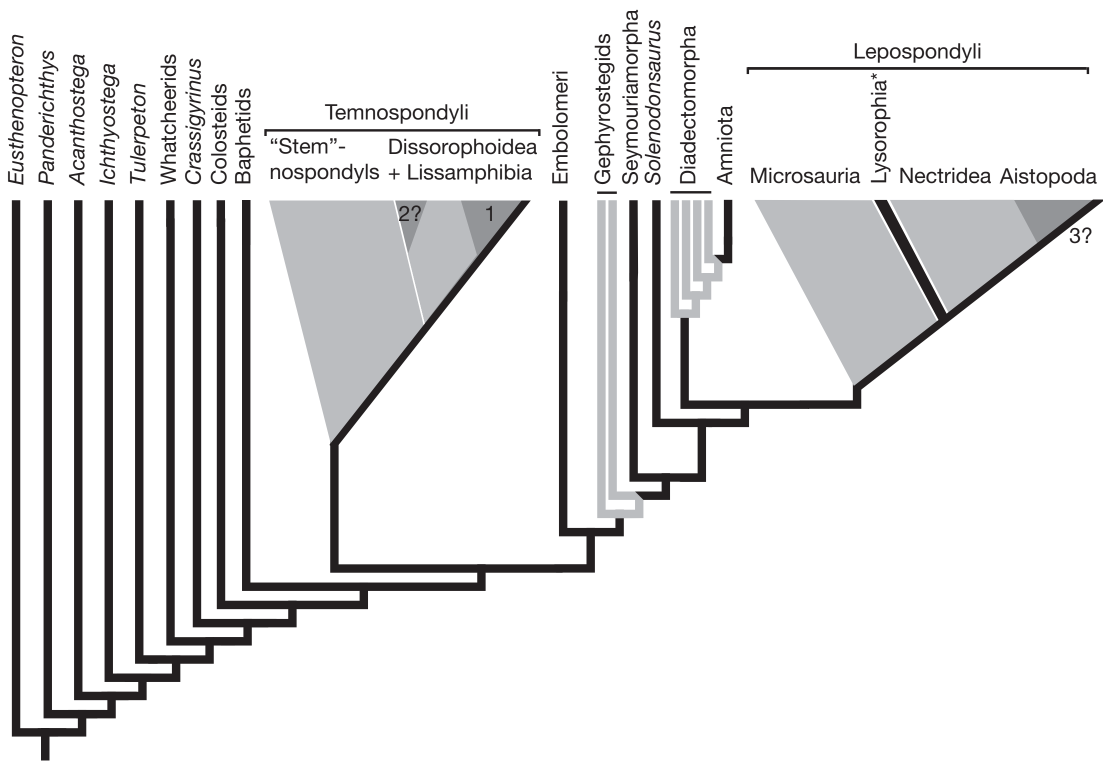

Fig. 5. — Taxonomic distribution of pedicellate teeth (in dark grey) in tetrapods on a synthetic phylogeny based on the hypothesis of Ruta & Coates (2007) showing one acquisition of this character among Amphibamid temnospondyls (**1**) and two other possible among Branchiosaurids (**2?**) and Aistopods (**3?**). Paraphyletic groups are in light grey and the term "stem"-nospondyls is a shortening of "stem-temnospondyls" that means "paleozoic temnospondyls that are not dissorophoids". The asterisk shows the alternative position of lissamphibians proposed by Laurin & Reisz (1997), Laurin (1998), and Vallin & Laurin (2004).

like *Montcellia* from the Stephanian of Montceau-les-Mines, are generally considered as aquatic (Bossy 1976), as the strong lengthening of the tail and its lateral flattening suggest. However, their rarity compared to branchiosaur remains mysterious (Dutuit & Heyler 1994). Urocordylids are very rare components of the aquatic faunas. According to Dutuit & Heyler (1994: 249): "Les observations taphonomiques indiquent un paléoenvironnement lacustre et un court transport des spécimens dans l'eau avant leur fossilisation." (taphonomic observations indicate a lacustrine paleoenvironment and a short transport of the specimens by water before their fossilization). Thus, all animals preserved in Montceau-les-Mines were either aquatic, or terrestrial and living close to the lakes.

It is often claimed that the loss of limbs may characterize an aquatic lifestyle. However, most extant limbless tetrapods are terrestrial: amphisbenians, snakes, anguidae, caecilians (Pough *et al.* 2004). Moreover, aquatic snakes exhibit a lateral flattening of the tail. Aistopods do not show this lateral flattening and do not have any structure that could indicate an aquatic lifestyle, e.g., grooves of the lateral line system, external gills. Even if they were aquatic, an elongate snake-like body easily allows the animal to come out of water and to move on land (as eels do for example, pers. obs.). Some authors also argued that aistopods were fossorial (Gregory 1948) but this has been refuted by Anderson (2002) who concluded that they were terrestrial lateral undulators.

Aistopods are among the first tetrapods to appear during the Carboniferous (with *Lethiscus* from the Visean of Scotland), and they may be the first that can be considered as terrestrial (Carroll 2000: 1256), although the lifestyle of geologically older tetrapods of the Early Carboniferous remains unclear (Thulborn *et al.* 1996; Clack & Carroll 2000; Clack 2002; Clack & Finney 2005).

CONCLUSIONS

The specimen MNHN-SOT-II-101076 represents the geologically youngest occurrence of the genus *Phlegethontia*, the second in Europe after those of Bohemia and the second in France after the vertebral column described by Heyler (1980). This juvenile specimen seems to bear pedicellate teeth, structures previously observed in a few dissorophoids, lissamphibians, and teleosts. This suggests that this character may have had a wider distribution and have been more homoplasic than previously suggested. The rarity of aistopods in the mainly aquatic faunal assemblage of Montceau-les-Mines indicates that they were probably terrestrial. If the earliest aistopods were also terrestrial, this would have repercussions on the early history of the conquest of land by vertebrates.

This study is also the first to analyse a nodule of Montceau-les-Mines by CT-Scan. This method has yielded complementary results to direct and SEM observation and was limited overall by the small size of the specimen. Scanning larger specimens would undoubtedly yield additional anatomical data. Thus, I strongly encourage CT-scan studies on the nodules of Montceau-les-Mines. This Lagerstätte has yielded more than 200 000 nodules (Poplin & Heyler 1994), scanning several of them would greatly increase our knowledge of this paleoecosystem and its peculiar taphonomy.

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APPENDIX

Data matrix. All the characters are from Anderson *et al.* (2003) except the new ones: 28, unique ossification of the posterior element of the mandible (0, absent; 1, present); 29, number of vertebrae (0, less than 70; 1, 70-90; 2, about 100; 3, from 120 up to 200; considered as additive).

Taxon/Character	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**
Lethiscus	0	0	0	0	0	0	0	1	1	0	?	?	0	0	0	0	0	1	0	1	0	?	1	1	0	0	0	0	1
Ophiderpeton	0	0	0	1	1	0	0	1	1	0	?	?	0	?	0	1	?	1	?	1	?	1	1	0	0	1	0	0	2
Oestocephalus	0	1	0	2	?	0	0	1	1	0	1	1	0	1	1	0	1	1	1	1	1	1	1	1	2	1	0	0	2
Phlegethontia longissima	1	?	1	2	?	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	0	1	1	1	1	2	1	1	3
P. linearis	1	?	1	2	?	1	1	1	1	1	?	?	1	1	0	0	?	0	1	1	0	1	1	1	1	2	1	1	3
Pseudophlegethontia	1	0	0	1	0	0	0	1	1	0	?	?	1	1	0	0	?	1	1	1	0	1	1	1	2	2	1	0	3
Scincosaurus	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Asaphestera	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Adelogyrinus	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Coloraderpeton	0	1	0	2	?	0	0	1	1	0	?	?	0	1	0	1	?	1	1	1	1	1	1	1	2	1	0	?	2
Brachydectes	0	1	0	2	?	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	?	0	1
Montcellian aistopod	1	?	?	?	?	?	1	?	?	1	1	?	1	?	?	?	?	1	1	1	?	?	?	?	?	?	?	1	?