

The branchiosaurid amphibians from the Lower Permian of Buxières-les-Mines, Bourbon l'Archambault Basin (Allier, France) and their biostratigraphic significance

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Key words. – Amphibia, Branchiosauridae, “Autunian”, French Massif Central, Taxonomy, Biostratigraphy.

Abstract. – Branchiosaurs are rare in the lacustrine fauna from the Lower Permian of Buxières-les-Mines (Massif Central, France). All known specimens belong to *Melanerpeton gracile*, which is significant for the *Melanerpeton gracile-Discosaurus pulcherrimus* zone in the biostratigraphical zonation of Upper Carboniferous and Lower Permian based on aquatic amphibians. This branchiosaurid species support the Asselian age (uppermost Lower “Autunian”/Rotliegend) of the Assise de Buxières in the Bourbon l'Archambault Basin (Allier, France).

Les Amphibiens branchiosauridés du Permien inférieur de Buxières-les-Mines, bassin de Bourbon l'Archambault (Allier, France) et sa signification biostratigraphique

Mots clés. – Amphibiens, Branchiosauridae, “Autunien”, Massif central, France, Taxonomie, Biostratigraphie.

Résumé. – Les Branchiosauridés sont rares dans la faune lacustre du Permien inférieur de Buxières-les-Mines, bassin de Bourbon l'Archambault (Massif central, Allier, France). Tous les spécimens connus appartiennent à *Melanerpeton gracile* qui est caractéristique de la zone à *Melanerpeton gracile-Discosaurus pulcherrimus* issue de l'échelle biostratigraphique basée sur les amphibiens aquatiques du Carbonifère supérieur et du Permien inférieur. Cette espèce de branchiosauridés permet l'attribution d'un âge assélien (juste au dessus de “l'Autunien inférieur”/Rotliegend) pour la série des schistes bitumineux de Buxières-les-Mines appartenant à l'assise de Buxières du bassin de Bourbon l'Archambault (Allier, France).

INTRODUCTION

The locality of Buxières-les-Mines is situated in the south-eastern part of the Permian basin of Bourbon l'Archambault (Aumance site) in the north of the Massif Central (fig. 1). Large opencast coal mines, abandoned since 2001, have disclosed the upper part of the Assise de Buxières. The formerly exposed 30 m to 40 m thick section starts with palustrine beds comprising the coal seams, followed by lacustrine bituminous black shales and fluvial fine clastics and channel sandstones at the top.

Our knowledge of the rich fauna and flora of Buxières-les-Mines has increased rapidly during the last decade [Steyer *et al.*, 2000]. Since the workshop on the Permian of Buxières-les-Mines in April 1997 an “European Convention for the Studies of the Buxières-les-Mines Fossiliferous Locality” was established and is working successfully [Pouillon and Steyer, 2001]. First results with new data on the flora and fauna of this locality were presented by Steyer *et al.* [2000]. Besides algae, stromatolites, palynomorphs and macroflora ; ostracods and blattoid insects (common *Compsoblattia* and rare *Spiloblattinidae*) were reported. The vertebrate fossils are of special importance. Orthacanthids, xenacanthids, hybodontids, acanthodians and actinopterygians are reported. Isolated scales of actinopterygians and

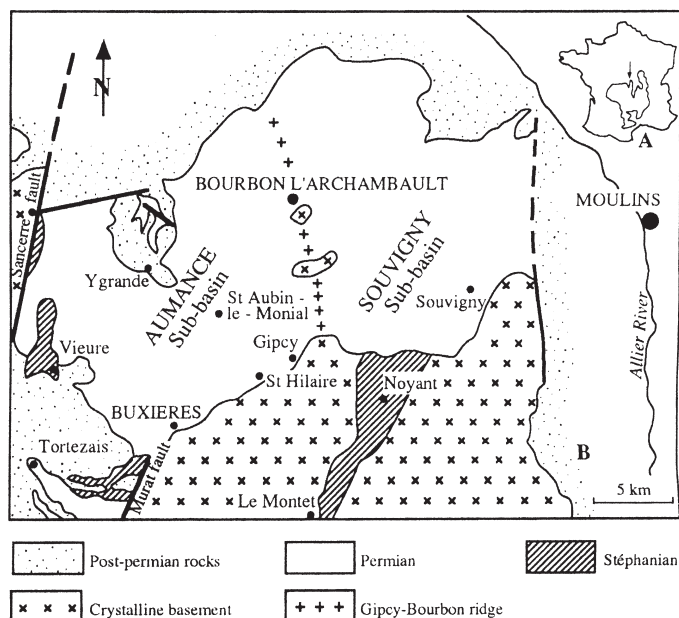


FIG. 1. – Geographical and geological setting. A. Location of the Bourbon-l'Archambault Basin. B. Simplified geological map of the Permian basin [after Paquette and Feys, 1989, modified from Steyer *et al.*, 2000].

FIG. 1. – Localisation géographique et géologique.

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spines of acanthodians are very frequent in the bituminous "fish shale".

The amphibian fauna consists of surprisingly large skeleton remains, which belong to the eryopid *Onchiodon* and the archeosaurid "*Cheliderpeton*". Both large-sized amphibians will be studied in detail by Steyer and Werneburg (in prep.)

The third represented amphibian group are the branchiosaurs. These nearly 5 to 7 cm long amphibians are unusually rare here in contrast to other occurrences of branchiosaurs in the basins of France or Germany. Up to now only 4 skeletons are known from the more clayish siltstones of Buxières-les-Mines. But the branchiosaurid amphibians are very interesting for biostratigraphy of the Permian in Europe [Werneburg, 1996].

SYSTEMATIC PALAEOLOGY

Order : Temnospondyli ZITTEL 1888
 Superfamily : Dissorophoidea BOLT 1969
 Family : Branchiosauridae FRITSCH 1879
 Genus : *Melanerpeton* FRITSCH 1878

Melanerpeton gracile (CREDNER 1881)

Occurrence. – Grey clayish siltstone between the pyroclastic horizons "Lien blanc" (Lb) and "Lien vert" (Lv) of the Assise de Buxières ("Autunian", Lower Permian) from the opencast mine near Buxières-les-Mines in the Bourbon l'Archambault Basin (Allier, France).

Material. – 4 specimens in the Paleontological Collection of Rhinopolis Association in Gannat with the following numbers : Bx 08.08.96/1 (mostly in dorsal, partly ventral aspect, fig. 3), Bx 18.07.00/3 (imprint of ventral and dorsal aspect, fig. 4), Bx 08.08.96/3 (in ventral aspect, but with imprint of dorsal skull roof bones, fig. 5) and Bx 26.04.96/1 (in dorsal aspect).

Diagnostic features :

1. Rough parasphenoid with a wide cultriform process and a large basal plate
2. Short and relatively tiny vomer
3. Occipital region very short (H_1)
4. Supratemporal very short, more short than wide
5. Blunt snout (short and wide)
6. Parietal relatively tiny
7. Postorbital short and wide
8. Squamosal short
9. Ilium robust with a wide dorsal process.

Description :

The four branchiosaurid specimens are small with a skull length from 6,5 mm up to 9 mm. The radial dermal sculpture of the dorsal skull roof is sometimes preserved on the imprint of frontal, parietal und supratemporal. The skull bones are well-ossified, if they are preserved. All specimens belong to one species (compare fig. 2-5 and table I), which was small.

Especially important is the shape of the long and narrow ectopteryoid and the long palatine (figs. 2 and 3). These

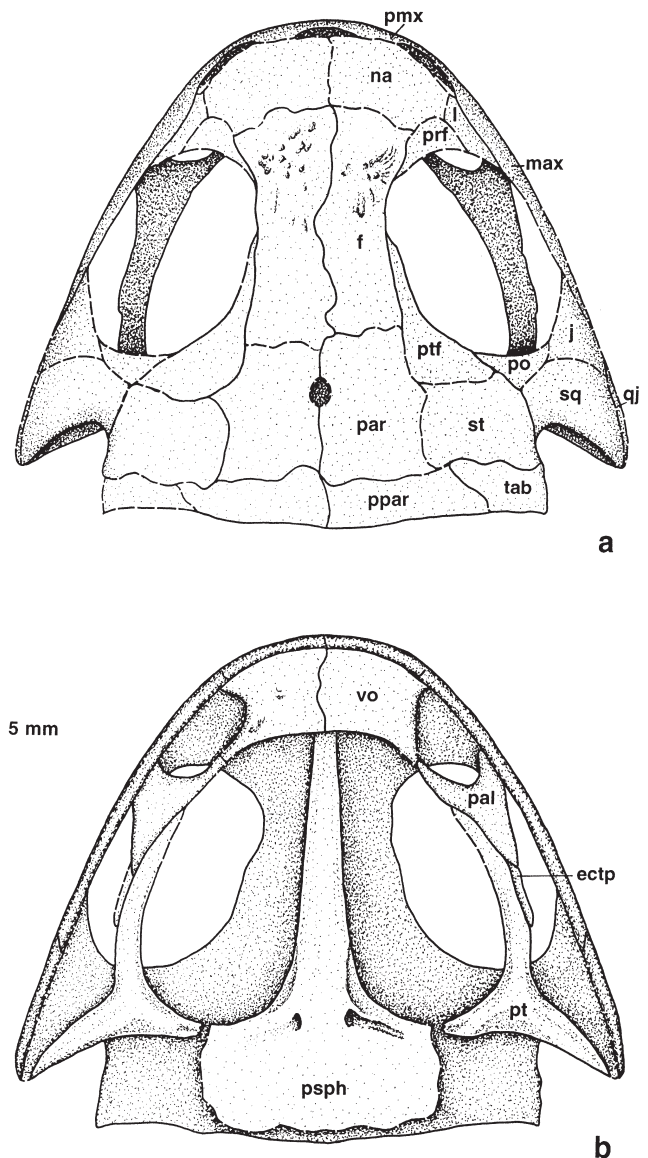


FIG. 2. – *Melanerpeton gracile* from the Assise de Buxières, reconstruction of dorsal skull roof and ventral palate.

(ectp – ectopterygoid, f – frontal, max – maxilla, pal – palatine, pmx – premaxilla, po – postorbital, ppar – postparietal, psph – parasphenoid, pt – pterygoid, ptf – postfrontal, sq – squamosal, st – supratemporal, tab – tabular, vo – vomer)

FIG. 2. – *Melanerpeton gracile* de l'Assise de Buxières, reconstitution du crâne et du palais.

features are characteristic for the genus *Melanerpeton* [compare Werneburg, 1986, 1989]. The ectopteryoid and palatine are longer and more narrow as in most specimens of *Melanerpeton gracile* from Saxony and the Thuringian Forest. But sometimes this shape is traceable within the variability of this species [compare Werneburg, 1988, fig. 4 f, g]. However, these features follow the tendency in the genus *Melanerpeton*. The interorbital region is narrow ($IO_w/S_1 = 0,24$, table I) and also diagnostic for this genus. The rough parasphenoid with a wide cultriform process and a large basal plate plus the short and relatively tiny vomer are characteristic for the species *Melanerpeton gracile* (in contrast to *Melanerpeton arnhardti/pusillum*-group and *Melanerpeton eisfeldi*).

TABLE I. – Biometric characters of *Melanerpeton gracile* from Buxières-les-Mines S_1 -skull length, IO_w -width of interorbital region, H_w/H_l -width/length of occipital region of skull table, HUM_l -length of humerus, Prswz-number of presacral vertebrae.

TABLE I. – Mesures de *Melanerpeton gracile*.

	fig. 5 Bx 08.08.96/3	fig. 3 Bx 08.08.96/1	fig. 4 Bx 18.07.00/3	Bx26.04.96/1
S_1	9,0 mm	7,5 mm	7,5 mm	6,5 mm
IO_w/S_1	0,24	0,24	-	-
H_w/S_1	-	-	0,82	0,74
H_w/S_1	0,38	0,32	-	-
HUM_l/S_1	0,39	0,47	0,47	-
Prswz	-	20 or 21	21 or 22	-

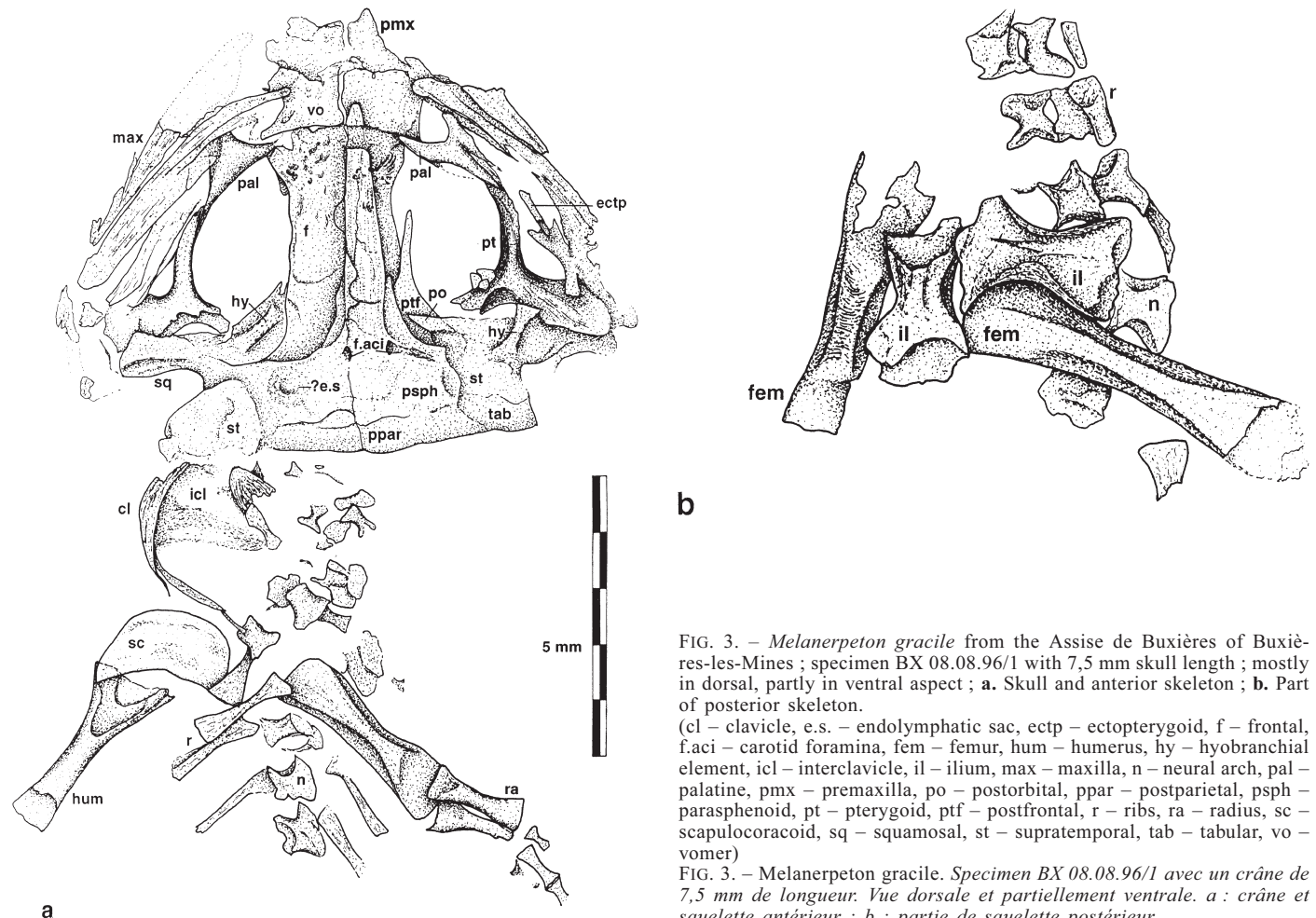
One stapes is preserved (fig. 5). The wide basal plate shows a large stapedia foramen and is continued in a short, narrower branch. A probable remain of an endolymphatic sac is traceable (fig. 3). Also some isolated bones of the hyobranchial apparatus are preserved (fig. 3).

The orbit is very long. The postfrontal is often large with an elongate posterior region (in contrast to *Melanerpeton arnhardi/pusillum*-group or *Apateon pedestris*, fig. 3, 5). Sometimes the postfrontal is narrower (fig. 4 and the fourth specimen BX 26.04.96/1.) and the postorbital is short. It may be slightly longer in correlation with the longer posterior part of the postfrontal. However the supratem-

poral is very short and wide in all four specimens, a condition known only in *Melanerpeton gracile* and *M. eisfeldi* (in contrast to *Melanerpeton arnhardi/pusillum*-group or *Apateon pedestris*). The distance from the posterior orbit up to the posterior postparietal margin is characteristically short in *Melanerpeton gracile* ($H_l/S_1 = 0,32-0,38$). The occipital region of the skull is wide (in contrast to *Melanerpeton pusillum*). The squamosal is relatively short (in contrast to *Melanerpeton eisfeldi*). The maxilla is of average length middle long and probably slightly longer than in the German *gracile*-material.

From the postcranial skeleton, the shape of the well-ossified ilium with the wide dorsal process (in contrast to *Branchiosaurus*, *Apateon intermedius*, *A. dracyiensis* or *Melanerpeton eisfeldi*) is important as a diagnostic feature. In figure 3 this bone is clearly visible, the ilium in figure 4 is overlapped by the femora and possibly the second ilium. The humerus is not very long, but relatively robust. The femur is longer than the humerus. The number of presacral vertebrae is 21 and possibly 22, as in *Melanerpeton gracile* and *M. pusillum* [Werneburg, 1989].

The specimens from Buxières-les-Mines clearly belong to the species *Melanerpeton gracile*, which is well known from the type locality Niederhäslich in the Döhlen-Basin near Dresden/Germany [Werneburg, 1991]. Many specimens of this species also are known from the Upper Oberhof Formation of the Thuringian Forest/Germany [Werneburg, 1988]. The specimens of both German occur-



b

FIG. 3. – *Melanerpeton gracile* from the Assise de Buxières of Buxières-les-Mines ; specimen BX 08.08.96/1 with 7,5 mm skull length ; mostly in dorsal, partly in ventral aspect ; a. Skull and anterior skeleton ; b. Part of posterior skeleton.

(cl – clavicle, e.s. – endolymphatic sac, ectp – ectopterygoid, f – frontal, f.aci – carotid foramina, fem – femur, hum – humerus, hy – hyobranchial element, icl – interclavicle, il – ilium, max – maxilla, n – neural arch, pal – palatine, pmx – premaxilla, po – postorbital, ppar – postparietal, psph – parasphenoid, pt – pterygoid, ptf – postfrontal, r – ribs, ra – radius, sc – scapulocoracoid, sq – squamosal, st – supratemporal, tab – tabular, vo – vomer)

FIG. 3. – *Melanerpeton gracile*. Specimen BX 08.08.96/1 avec un crâne de 7,5 mm de longueur. Vue dorsale et partiellement ventrale. a : crâne et squelette antérieur ; b : partie de squelette postérieur.

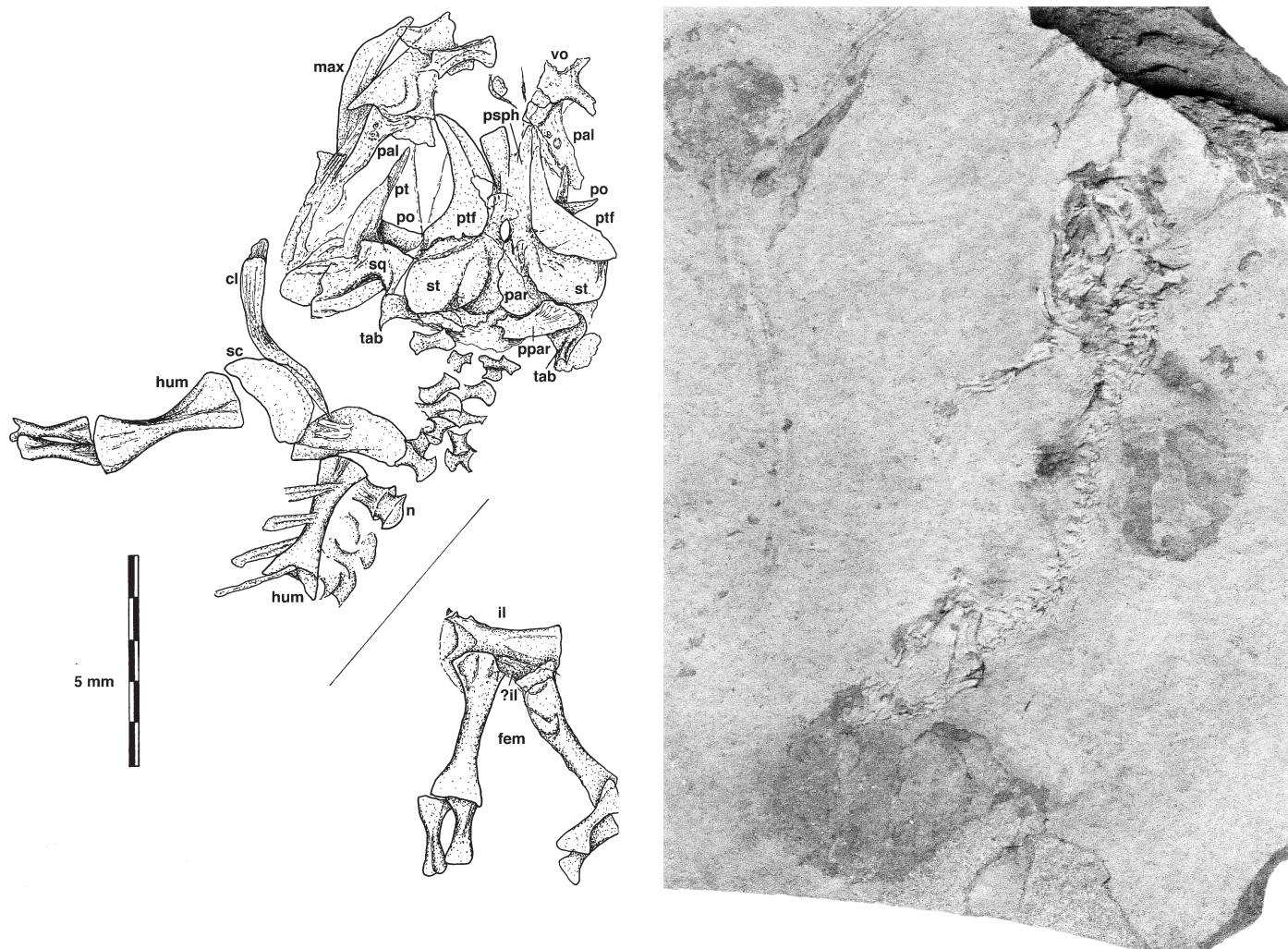


FIG. 4. – *Melanerpeton gracile* from the Assise de Buxières of Buxières-les-Mines ; specimen BX 18.07.00/3 with 7,5 mm skull length ; skull with anterior and posterior skeleton ; imprint of ventral and dorsal aspect.

(cl – clavicle, fem – femur, hum – humerus, il – ilium, max – maxilla, n – neural arch, pal – palatine, po – postorbital, ppar – postparietal, psph – parasphenoid, pt – pterygoid, ptf – postfrontal, sc – scapulocoracoid, sq – squamosal, st – supratemporal, tab – tabular, vo – vomer)

FIG. 4. – *Melanerpeton gracile*, specimen BX 18.07.00/3 ; crâne avec squelette antérieur et postérieur ; moulage ventral et dorsal.

rences differ in some small features, so Werneburg [1988] created two geographically isolated subspecies : *Melanerpeton gracile gracile* from the Döhlen Basin and *M. gracile thuringense* from the Thuringian Forest Basin. With only 4 specimens from Buxières-les-Mines the subspecies could not be determined with certainty.

Werneburg discussed the first branchiosaur from Buxières as *Melanerpeton ? gracile* in Steyer *et al.* [2000]. Now this prognosis is demonstrated by 3 further specimens.

BIOSTRATIGRAPHY

The biostratigraphical position of the series of the upper part of the Assise de Buxières in the Aumance Sub-basin of the Bourbon l'Archambault-Basin (fig. 1) has been under discussion for some years now [Steyer *et al.*, 2000]. The flora shows coexistence of the "Stephanian and Autunian type" [Broutin *et al.*, 1990]. Studies on blattoid insect

wings and isolated shark teeth are in preparation by J. W. Schneider.

The branchiosaurid species *Melanerpeton gracile* is an important form in the biostratigraphical zonation (fig. 7) of the Upper Carboniferous and Lower Permian based on aquatic amphibians [Werneburg, 1989, 1996]. This zonation is well founded on several parts of phylo(morpho)genetic lineages of two or three species especially from branchiosaurid, micromelerpetontid and discosauriscid amphibians. From the genus *Melanerpeton* we know two parallel lineages. One lineage includes the Upper Carboniferous species *Melanerpeton sembachense*, followed by *M. eisfeldi* and the youngest known species of this lineage *M. gracile* (fig. 6, 7).

The species *M. gracile* characterises together with the basal discosaur the *Melanerpeton gracile-Discosauriscus pulcherrimus* zone, which is known from the following occurrences :

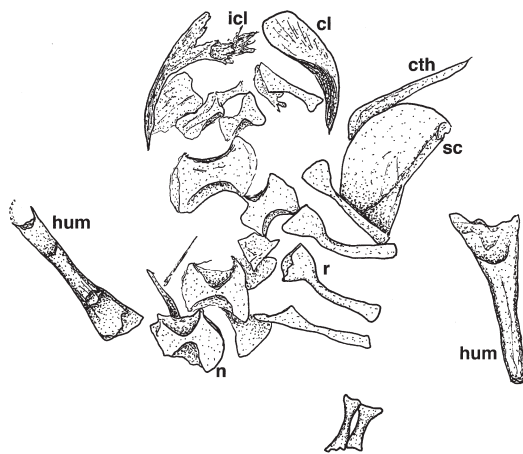
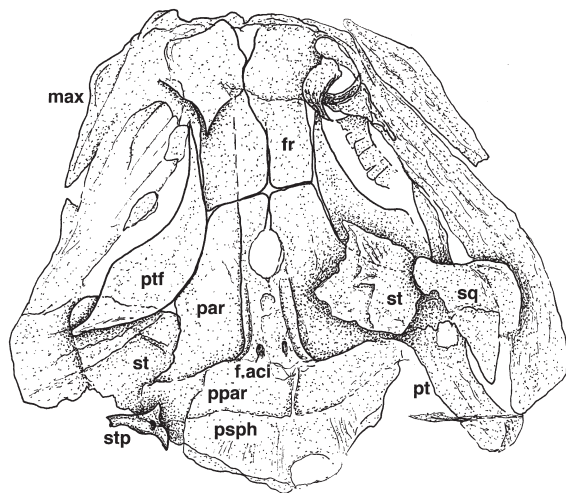


FIG. 5. – *Melanerpeton gracile* from the Assise de Buxières of Buxières-les-Mines ; specimen BX 08.08.96/3 with 9 mm skull length ; mostly in dorsal, partly ventral aspect ; skull with anterior skeleton, stapes is preserved in the counterpart.

(cl – clavicle, cth – cleithrum, f – frontal, f.aci – carotid foramina, hum – humerus, icl – interclavicle, max – maxilla, n – neural arch, ppar – postparietal, psp – paraspinal, pt – pterygoid, ptf – postfrontal, r – ribs, sc – scapulocoracoid, sq – squamosal, st – supratemporal, stp – stapes)

FIG. 5. – *Melanerpeton gracile*, specimen BX 08.08.96/3 avec un crâne de 9 mm de longueur.

- Niederhäslich Formation of the Döhlen Basin, Germany
- Upper Oberhof Formation of the Thuringian Forest Basin, Germany
- Olivétin Formation of the Intrasudetic Basin, Bohemia
- Upper part of the Assise de Buxières from Buxières-les-Mines in the Bourbon l'Archambault Basin, France
- “Paperslate” from Bourbon l'Archambault in the Bourbon l'Archambault Basin, France
- Top of the Meisenheim Formation (L-0 10) of the Saar-Nahe Basin, Germany.

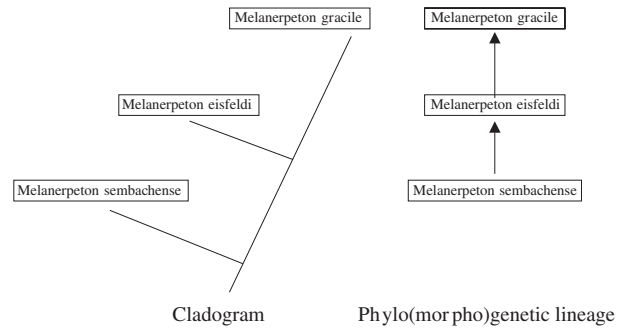


FIG. 6. – The pattern of cladogram and their simplified version as phylo(morpho)genetic lineage of *Melanerpeton* with the same biostratigraphic significance.

FIG. 6. – Cladogramme et lignée phylo(morpho) génétique de *Melanerpeton*.

Some indications of new occurrences of this zone are known from the Blanzly and Autun Basins in France, which will be published in the near future.

The *Melanerpeton gracile* described here indicates an Asselian age (uppermost Lower “Autunian”/Rotliegend) for the Upper Buxières Formation using the biostratigraphical zonation with amphibians. It is possible to correlate the Buxières-les-Mines locality with many other occurrences in Europe (see above). In comparison to the Thuringian Forest section the upper part of the Assise de Buxières could be of Lower or Upper Oberhof Formation age or only slightly younger (because the branchiosaurs disappear almost completely in Central Europe). This is in good agreement with other biostratigraphic and isotopic data (Schneider *et al.* in preparation). Therefore, it seems to be an example to demonstrate the practical advantage of using European Paleozoic amphibians as stratigraphic markers.

In contrast to these results Steyer [2000] published some other hypotheses in this journal, which are necessary to address with some notes here.

1. Unfortunately his theoretical statements are not the result of studies of the original material from *Sclerocephalus*, branchiosaurs, micromelerpetontids, Russian Permian dissorophoids, seymouriamorphs, anthracosaurs or tetrapod footprints. It would be useful, to work first on these groups, before looking for supposed mistakes in the research of the last 15 years.

2. Steyer [2000] reviewed a lot of references in some sentences or pages only. He mixed taxonomic details from earlier contributions [for instance Boy, 1987], which are partly revised now, with more new concepts. His figure 4 (with 5 “citation-mistakes”) shows two biozonations based on amphibians which should be demonstrate the “disaster” in the German basins. But it is necessary to know that the biozonation of Boy [1987] was established by the mostly endemic amphibian species of the Saar-Nahe Basin and therefore this zonation is valid up to now only for this basin. The biozonation of Werneburg [1989, 1996] is based on species which are known from many basins in Europe, so the differences between both zonation are normal.

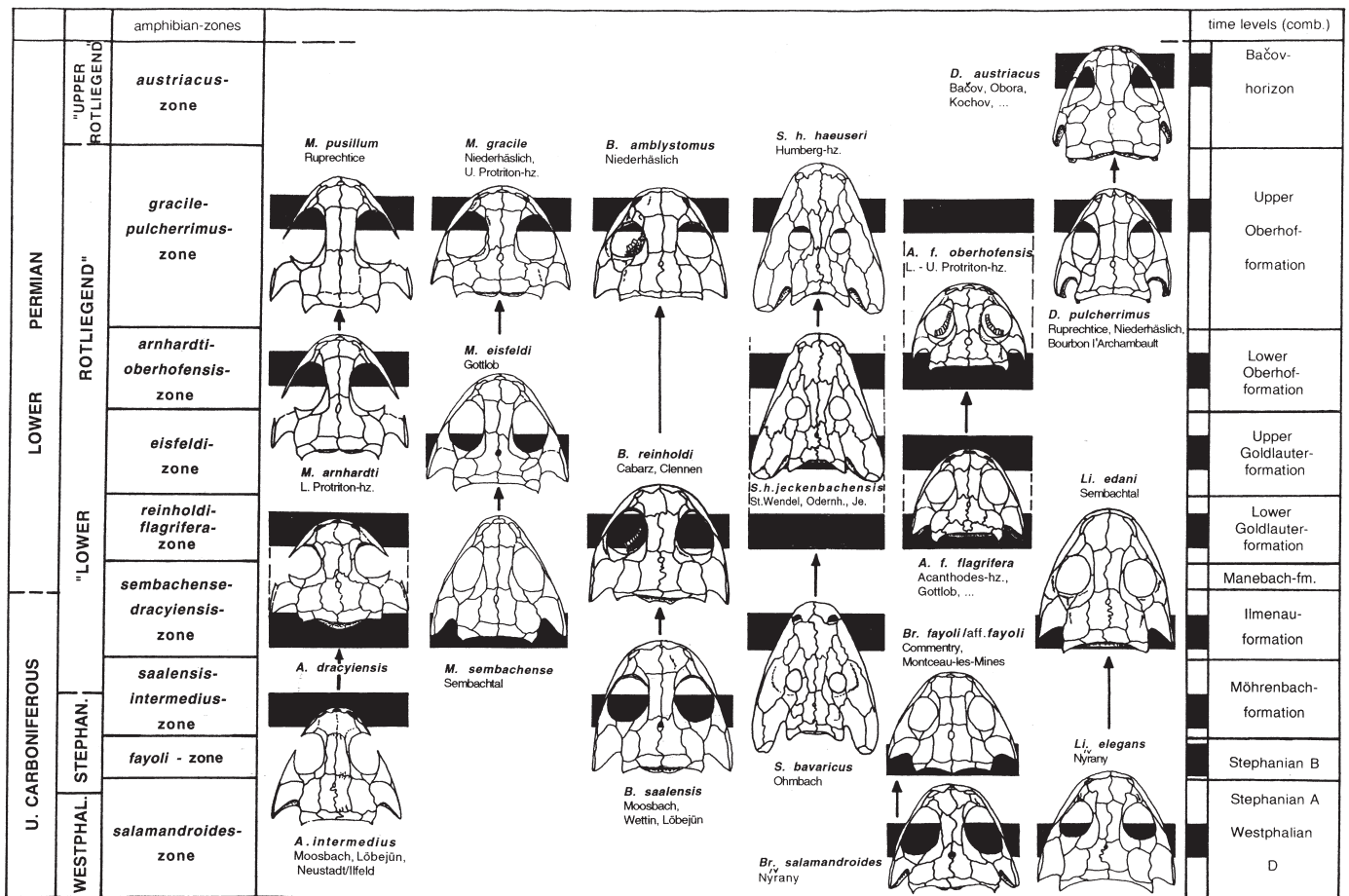


FIG. 7. – Biostratigraphic zonation based on aquatic amphibians for the European Upper Carboniferous and Lower Permian [Werneburg, 1996]. (A. – Apateon, B. – Branchierpeton, Br. – Branchiosaurus, D. – Discosauriscus, Li.– Limnogyrinus, M.– Melanerpeton, S.– Sclerocephalus).
 FIG. 7. – Répartition biostratigraphique des amphibiens aquatiques du Carbonifère supérieur et Permien inférieur d'Europe [Werneburg, 1996].

3. Precise biostratigraphic correlations are only possible on the base of the species or subspecies level, which is integrated in phylo(morpho)genetic lineages-relations. The basic concept is the consecutive range of species with (more or less) well known first (FAD) and last (LAD) appearance datum, simplified in the biostratigraphic zonation scheme of figure 6.

Ichnospecies of tetrapod footprints indicate osteological families or genera. So the scale for biostratigraphic correlations is much larger, and not very sharp, if we use families, genera or isolated species for comparisons.

4. It is easy to criticize the status of subspecies in general because only some small differences are characteristic for these taxa. More complete fossil record will allow a revision or validity of this taxa. However, this must be based on the type specimens and original material as well and increasingly more samples too. So it could be in the cases of subspecies from *Sclerocephalus haeuseri*, *Apateon pedestris* or *Apateon flagrifera*. However, these are only 2 of 9 lineages on which the biozonation of Werneburg [1996, here fig. 7] is based. So it is solely a peripheral and no essential problem of zonations with Paleozoic amphibians.

5. Two last comments. Steyer [2000] pointed out that the biostratigraphical important seymouriamorph *Discosauriscus pulcherrimus* [Werneburg and Kiersnowski, 1996] would have a questionable validity. But he does not know the coexistence of both species, *D. pulcherrimus* and *D. austriacus*, in the Bačov Horizon of the Boskovice Furrow/Moravia [Klembara, 1997]. So both papers pointed out the validity of both discosauriscid species in contrast to Steyer[2000].

Steyer criticized the imprecise results with an uncertainty of 10 million years for the Permian of India [Werneburg and Schneider, 1996] or for the Permian of Sardinia [Ronchi and Tintori, 1997]. The amphibians of the Kashmir Permian are not included in phylogenetic lineages up to now. Their evolutionary biogeographical status remains unique. Therefore a precise age could not be given of course. In the other case of the Permian amphibians of Sardinia new studies of the original material will allow us a better understanding of their taxonomy and a much more precise biostratigraphic correlation [Freytet *et al.*, 2002, Werneburg and Ronchi, in prep.].
 Work, work, work is necessary to solve the biostratigraphic problems !

CONCLUSIONS

A diverse flora and fauna is known from the series of the upper part of the Assise de Buxières-les-Mines of the Bourbon l'Archambault Basin, especially fishes and amphibians. A great number of large amphibians, but also four small branchiosaurid skeletons are discovered here. All branchiosaurid specimens, which are characterized by 9 preserved diagnostic features, clearly belong to the species *Melanerpeton gracile*. *M. gracile* represents the youngest form of a lineage, therefore, the first appearance datum (FAD) is well known and could be used easily for precise biostratigraphic correlations in Europe [Werneburg, 1996]. It belongs to the *Melanerpeton gracile-Discosaurus*

pulcherrimus zone and indicates an uppermost Lower "Autunian"/Rotliegend age (Asselian).

Biostratigraphic results with amphibians were presented for the Permian carboniferous basins for nearly 15 years. However, it is necessary to qualify the biozonations with amphibians step by step through new investigations with original material.

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