PALÆO VERTEBRATA

# Lissamphibians from Dams (Quercy, SW France): Taxonomic identification and evolution across the Eocene-Oligocene transition

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**Abstract**: The locality of Dams (Quercy, southwestern France) has yielded two fossil assemblages, one from the late Eocene and another from the early Oligocene, making it one of the few localities with infillings across the Eocene-Oligocene transition. At least 24 taxa (13 mammals, 11 snakes) have been identified in this locality. Study of the lissamphibian remains from Dams yields an Eocene and an Oligocene assemblage, with a total of eight taxa. The Eocene assemblage includes two unnamed salamandrine species, one unnamed pelobatid species and one pyxicephalid species (*Thaumastosaurus*). The Oligocene assemblage includes two unnamed pleurodeline species, one salamandrine species (*Salamandra sansaniensis*) and an unnamed pelobatid species. Among the eight taxa from Dams, one Eocene salamandrine and one Oligocene pleurodeline are identified for the first time in the Quercy. A review of the lissamphibians from the Quercy area identifies eleven taxa for the Late Eocene (MP19) and eight taxa for Early Oligocene (MP22), with a major turnover at the Eocene-Oligocene transition. This turnover occurs in a time of major climatic changes, with a significant decrease in temperature and precipitation and concurrent increase in seasonality in Europe, likely affecting specialized taxa.

**Keywords**: Quercy Phosphorites, Grande Coupure, Lissamphibia, Eocene-Oligocene

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## INTRODUCTION

The Quercy Phosphorites area provides more than 200 fossiliferous karstic infillings localities in southwestern France (Pélissié *et al*., 2021). These localities have produced a rich diversity of vertebrate assemblages ranging from the early Eocene to the Early Miocene, with most localities centered around the late Eocene-middle Oligocene (Pélissié *et al*., 2021). Due to the depositional environment (karstic infillings), lissamphibian fossils are rare in the Quercy Phosphorites (Rage, 2006, 2012, 2016), even compared to other components of the herpetofauna, especially lizards and snakes (Augé, 2005; Rage, 2006). Furthermore, the fragmentary nature of the material makes the identification of isolated lissamphibian bones, especially for anurans, difficult below the family level. Lastly, lissamphibians, especially salamanders, from the Quercy have been poorly studied, with almost no taxonomic work realized over the last three decades (Duffaud, 2000; Rage, 2006, 2016). As such, the Quercy area has revealed limited insight on the diversity of Eocene and Oligocene lissamphibians and their evolution. The few available studies suggested a large turnover around the Eocene-Oligocene transition, with a high level of extinction rate among both salamanders and anurans at the end of the Eocene (Rage, 2006, 2016; Vasilyan, 2018). An important mammalian turnover also occurs at this transition, referred to as the "Grande Coupure" (Stehlin 1909; Escarguel *et al*. 2006; Weppe *et al*. 2024), enhanced by major climatic and tectonic changes. The Dams phosphate pit in the commune of Caylus (Quercy, Tarn et Garonne) presents an interesting opportunity to enhance our knowledge of lissamphibian diversity in the Quercy area at the "Grande Coupure". It houses four distinct karstic infillings, two dated from the late Eocene (DAM1, DAM2; MP19) and two from the early Oligocene (DAM3, DAM4; MP22; Weppe *et al*., 2020). Here we identify and describe the late Eocene and early Oligocene lissamphibian assemblages from Dams. We then compare both assemblages to other contemporary localities and discuss the evolution of lissamphibian diversity evolution across the Eocene-Oligocene transition in the Quercy area.

## MATERIALS AND METHODS

**Abbreviations**: DAM1, DAM2, DAM3, DAM4: localities of Dams; UM, University of Montpellier. All specimens are housed in the collection of the University of Montpellier (Montpellier, France) under the collection numbers UM-DAM1-/ UM-DAM2-/ UM-DAM3- and UM-DAM4-.

**Anatomical nomenclature**: For anurans, the nomenclature used is derived from Lemierre *et al*. (2021). For salamanders, the nomenclature is derived from Macaluso *et al*. (2023).

## SYSTEMATIC PALAEONTOLOGY

Lissamphibia Haeckel, 1866
Urodela Duméril, 1805
Salamandridae Goldfuss, 1820
Salamandrinae Fitzinger, 1843

Unnamed salamandrine A
Fig. 1A–C
**Referred specimen**: UM-DAM1-334, one trunk vertebra.

**Description**: UM-DAM1-334 is opisthocoelous (Fig. 1B). The centrum is elongated anteroposteriorly and a slight constriction marks the boundary between the anterior condyle and the centrum (Fig. 1A, B). The neural arch is flattened anteriorly and vaulted posteriorly (i.e., the portion of the neural arch dorsal to the postzygapophyses represents one-fifth of the total vertebra height; Fig. 1C). The anterior margin of the neural arch is notched at mid-width, making the anterior condyle visible in dorsal view (Fig. 1A). The prezygapophyses are large and ovoid (Fig. 1A). The neural crest seems to be moderately developed anteriorly as a thin, blade-like ridge, but it does not extend posteriorly on the entire neural arch length (ends before reaching the posterior margin of the neural arch; Fig. 1A). The neural crest reaches its peak height at midlength (Fig. 1C). The posterior margin of the neural arch bears two poorly developed posterior bulges (Fig. 1A). This margin does not bear any incisura dorsalis (i.e., posterior cotyle visible in dorsal view; Fig. 1A). In lateral view, the anterior zygapophyseal crest extends posteroventrally to the dorsal surface of the diapophysis (Fig. 1C). A well-developed anterior alar process is present anterolaterally, connecting the base of the prezygapophysis with the parapophysis (Fig. 1C). It delimits, with diapophysis and parapophysis, a lateral fossa (Fig. 1C). Both dia- and parapophyses are distinguishable from each other (i.e., they form bicipital transverse processes) and are connected by a thin lamina (Fig. 1C). Although not fully preserved distally, the diapophysis is hollow. The diapophyses and parapophyses are oriented posterolaterally (Fig. 1A). In ventral view, the centrum is badly preserved, although a pair of subcentral foramina are evident at midlength (Fig. 1B). The anterior and posterior ventral crests are broken, so their development and extension are unknown (Fig. 1B).

**Attribution**: The presence of bicipital transverse processes and likely distally hollow dia- and parapophyses and the opisthocoelous centrum allows for an assignment of UM-DAM1-334 to the Salamandridae (Macaluso *et al*., 2022). UM-DAM1-334 is excluded from the strange *Phosphotriton* in having an opisthocoelous centrum (Tissier *et al*., 2016). Among European extinct and extant salamandrids, two subfamilies, the Salamandrinae and Pleurodelinae are recognized. UM-DAM1-334 is reminiscent of extant pleurodelines and *Salamandra* in having a marked anterior zygapophyseal crest in lateral view (Macaluso *et al*., 2023). However, UM-DAM1-334 is also reminiscent of *Salamandra* in (1) having a small constriction marking the base of the anterior condyle and (2) being strongly dorsoventrally compressed (Macaluso *et al*., 2023). It also exhibits a unique characteristic of Salamandrinae, having the peak of the neural crest at midlength (Macaluso *et al*., 2023). Thus, UM-DAM1-334 is assigned to the subfamily Salamandrinae. UM-DAM1-334 is similar to an illustrated vertebra assigned to "Salamandridé C" by Duffaud (2000: fig. 37). Thus, UM-DAM1-334 could be referred to the informal "Salamandridé C". However, we prefer to informally identify UM-DAM1-334 as "Unnamed salamandrine A".

Unnamed salamandrine B

Fig. 1D–H

**Referred specimen**: UM-DAM2-24, one trunk vertebra.

**Description**: The vertebra is smaller than UM-DAM1-334 and poorly preserved, missing most of the transverse processes (Fig. 1E). The centrum is opisthocoelous with a moderately developed anterior condyle (Fig. 1D, H). A slight constriction marks the boundary between the anterior condyle and the centrum. The neural arch is flattened dorsoventrally, with the portion of the neural arch dorsal to the postzygapophyses representing one-fifth of the total vertebra height (Fig. 1E, F). The neural crest is reduced to a faint ridge that fails to reach the posterior margin of the neural arch (Fig. 1G). The anterior margin of the neural arch is deeply notched (anterior condyle fully visible in dorsal view; Fig. 1G). The prezygapophyses extend anterolaterally at a shallow angle (Fig. 1G). The lateral surface lacks a dorsal alar process, and the preserved base of

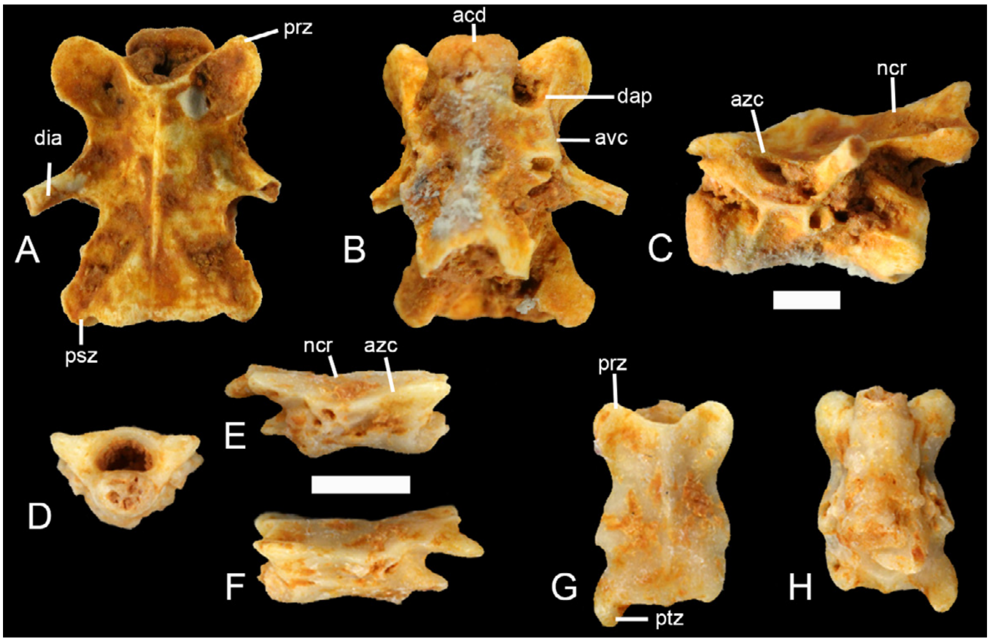

**Figure 1.** Eocene Salamandrinae (Salamandridae) of Dams. **A–C**, UM-DAM1-334, trunk vertebra of the unnamed salamandrine A ("Salamandridé C") in A, dorsal, B, ventral and C left lateral views; **D–H**, UM-DAM2-24, trunk vertebra of the unnamed salamandrine B in D, anterior, E, right lateral, F, left lateral, G, dorsal and H, ventral views. Images at different magnification, see corresponding 1 mm scale bars. Abbreviations: acd, anterior condyle; avc, anterior ventral crest; azc, anterior zygapophyseal crest; dap, dorsal alary process; dia, diapophysis; ncr, neural crest; prz, prezygapophysis; ptz, postzygapophysis.

the dia- and parapophyses show they were strongly oriented posterolaterally (Fig. 1F).

**Attribution**: UM-DAM2-24 differs from UM-DAM1-334 in (1) having a more dorsoventrally compressed neural arch and (2) a slender and elongated centrum. It is assigned to the Salamandridae on the basis of an opisthocoelous centrum. It is reminiscent of the extant European salamandrine *Chioglossa* and *Mertensiella* in having a dorsoventrally compressed and very elongated (anteroposteriorly) vertebra (Ratnikov and Litvinchuk, 2007; Macaluso *et al.*, 2023). UM-DAM2-24 differs from *Mertensiella* in having its zygapophyses less extended laterally (Ratnikov and Litvinchuk, 2007). Our specimen differs from *Chioglossa* in having a smaller neural canal in anterior view. Thus, UM-DAM2-24 cannot be assigned to any extant salamandrine genera. Hence, we assign UM-DAM2-24 to a second indeterminate salamandrine from the Eocene and is informally identified as “unnamed salamandrine B”.

*Salamandra* Garsault, 1764

*Salamandra sansaniensis* Lartet, 1851

Fig. 2

**Referred specimen**: UM-DAM4-3, one trunk vertebra.

**Description**: UM-DAM4-3 is a large vertebra (9 mm long; Fig. 2). The centrum is opisthocoelous with an anterior condyle bearing a marked constriction at its base (Fig. 2A, F). The vertebra is not elongated (width subequal to its length; Fig. 2). The neural arch is flattened dorsoventrally and the entire vertebra is flattened (one fifth of the height of the vertebra is made by the neural arch region dorsal to the postzygapophyses; Fig. 2C, D). The anterior margin of the neural arch is notched (Fig. 2E). A faint low neural crest is present and visible in lateral view on the anterior and mid portion of the neural arch (Fig. 2C, E). The prezygapophyses are large and expand anterolaterally (Fig. 2E). The posterior margin of the neural arch bears two small posterior projections (Fig. 2E). The anterior and posterior prezygapophyseal crests are marked in lateral view. The diapophyses and parapophyses are distinguishable but are broken at their base (Fig. 2C), they were likely oriented posteriorly (Fig. 2C). In ventral view, the ventral surface of the centrum is pierced by several foramina (Fig. 2F). The anterior and posterior ventral crests are preserved (Fig. 2F). The former is more developed than the latter, making the ventral lamina an asymmetrical rhomboidal shaped structure (Fig. 2F).

**Attribution**: UM-DAM4-3 is assigned to the Salamandridae based on the presence of bicipital transverse processes. It can be assigned to the Salamandrinae on its width subequal to its length (absent in several salamandrine genera and pleurodelines; Ratnikov and Litvinchuk, 2007; Macaluso *et al.*, 2023). UM-DAM4-3 is similar to two genera of salamandrines, *Megalotriton* and *Salamandra*, both present in the Quercy (Duffaud, 2000; Rage, 2006) on the following characters: (1) straight anterior zygapophyseal crest visible in lateral view; (2) vertebra not elongated, with width subequal to its length; (3) vertebra dorsoventrally flattened; and (4) reduced neural crest. Both have been mentioned in the early Oligocene of the Quercy (albeit the assignment to *Megalotriton* has been questioned; Rage and Augé, 2015). UM-DAM4-3 differs from vertebrae assigned to *Megalotriton* in (1) being smaller; (2) not being wider than long; (3) thinner diapophyses and parapophyses; (4) diapophyses and parapophyses inserted more posteriorly; and (5) zygapophyses less expanded laterally (Duffaud, 2000). It does however resemble the extinct *Salamandra sansaniensis* in (1) having the vertebral width subequal to its length; (2) having two small posterior projections on the posterior margin of the neural arch; (3) reduced neural crest and (4) thin diapophyses and parapophyses oriented posteriorly (Duffaud, 2000; Rage and Augé, 2015). Thus, we assign UM-DAM4-3 to *Salamandra sansaniensis*.

Salamandrinae indet.

Fig. 3

**Referred specimen**: UM-DAM4-2, one posterior trunk vertebra.

**Description**: UM-DAM4-2 is large (2 mm centrum’s length) opisthocoelous trunk vertebra (Fig. 3). The vertebra is moderately elongate, with a slight constriction marking the boundary between the anterior condyle and the centrum (Fig. 3A, C, F). The anterior condyle is not visible in dorsal view, but this is due to breakage (i.e., anteriormost portion of the condyle is missing; Fig. 3C, E). The neural arch is mostly flattened dorsoventrally, with the posterior region slightly vaulted (Fig. 3A, C). The neural arch portion dorsal to the postzygapophysis represents one-fifth of the vertebra heigh. The neural crest is moderately developed and blade-like, starting just behind the anterior margin of the neural arch and extending posteriorly to the posterior margin of the neural arch (Fig. 3D, E). The prezygapophyses are not markedly expanded laterally, almost circular shaped (Fig. 3E). The preserved left postzygapophysis

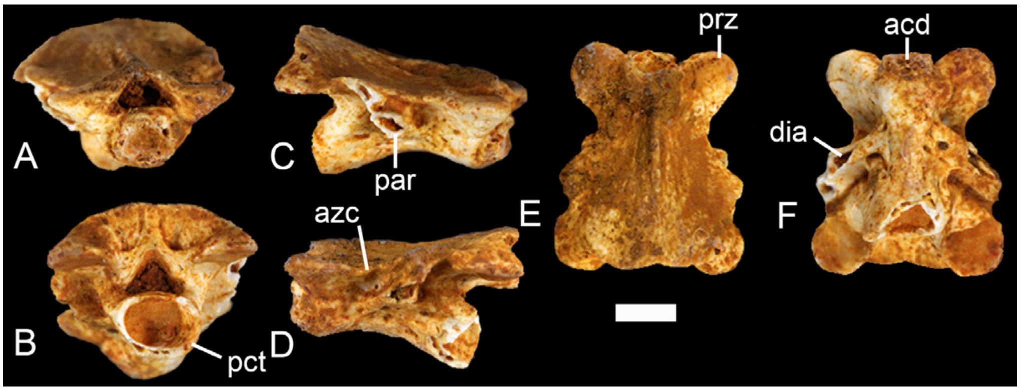

**Figure 2.** Oligocene salamandrine (Salamandridae) of Dams. **A–F**, UM-DAM4-3, trunk vertebra of *Salamandra sansaniensis* in A, anterior, B, posterior, C, right lateral, D, left lateral, E, dorsal and F, ventral views. Scale bar equals 1 mm. Abbreviations: acd, anterior condyle; azc, anterior zygapophyseal crest; dia, diapophysis; par, parapophysis; pct, posterior cotyle; prz, prezygapophysis.

is markedly expanded posteriorly (Fig. 3E). The anterior zygapophyseal crest is straight and well-marked laterally, contacting the dorsal surface of the diapophysis (Fig. 3C, D). Both dia- and parapophyses are distinguishable but separated by a short and thin lamina (Fig. 3D). They are posteriorly oriented. The incisura vertebralis caudalis is deep and contacts the centrum (Fig. 3C, D). The ventral surface of the centrum is pierced by numerous small foramina (Fig. 3F). The anterior and posterior ventral crests are poorly preserved, so their lateral expansion cannot be assessed (Fig. 3F).

**Attribution**: The presence of (1) bicipital transverse processes (Salamandridae) and (2) an opisthocoelous centrum warrant assignment to Salamandridae. UM-DAM4-2 is almost identical to *Salamandra sansaniensis*, but differs by its smaller size, its more elongated neural arch and centrum. In addition, the anterior condyle is poorly preserved, and one main characteristic, the peak of the neural crest at its midlength, is not possible to observe. Hence, we assign UM-DAM4-2 to Salamandrinae indet., although it could belong to *Salamandra sansaniensis*.

Pleurodelinae Tschudi, 1838

Unnamed pleurodeline A

Fig. 4A–E

**Referred specimen**: UM-DAM4-1, one trunk vertebra.

**Description**: UM-DAM4-1 is a small vertebra (1.5 mm centrum's length; Fig. 4A–E). The centrum is opisthocoelous, with a slight constriction marking the boundary between the anterior condyle and the centrum (Fig. 4A, E). Most of the anterior portion of the neural arch is missing, but the vertebra does not appear to have been compressed dorsoventrally (i.e., one-third of the vertebra height is formed by the neural arch portion dorsal to the postzygapophyses, Fig. 4C). The neural crest is moderately developed on the preserved mid- and posterior region (Fig. 4C, D). It does not vary in height and extends back to the posterior margin of the neural arch (Fig. 4C). It seems to thicken on its dorsoposterior portion and might be bifid (Fig. 4D). The anterior prezygapophyseal crest is visible in lateral view and contacts the diapophysis dorsally (Fig. 4C). An anterior alar process seems present (Fig. 4C). A lateral fossa could be present but is covered by sediment (Fig. 4C). Both dia- and parapophyses are distinguishable (bicipital transverse processes) and separated by an oblique lamina (Fig. 4A, C). The anterior and posterior ventral crests are well developed laterally, forming an asymmetrical rhomboid structure (Fig. 4E).

**Attribution**: UM-DAM4-1 is assigned to the Pleurodelinae based on the following features: (1) bicipital transverse processes and opisthocoelous centrum (Salamandridae) and (2) marked anterior zygapophyseal crest. It resembles "Salamandridé F" of Duffaud (2000) in (1) having a moderately to well-developed neural crest, extending up to the posterior margin of the neural arch; (2) thickened posterior part of the neural crest; (3) well developed anterior condyle with a marked constriction at its base. However, the dia- and parapophyses and neural crest seem thinner, making it more similar to "Salamandridé G" (if Duffaud's 2000 description is correct). It also shares with "Salamandridé G" the presence of large subcentral foramina (absent in "Salamandridé F"; Duffaud, 2000).

UM-DAM4-1 resembles the extant *Calotriton* (Macaluso *et al*., 2023: fig. 10E), *Euproctus* (Macaluso *et al*., 2023: fig. 11A), *Lissotriton* (Ratnikov and Litvinchuk, 2007: figs. 11, 12; Macaluso *et al*., 2023: fig. 11C) and *Ommatotriton* (Ratnikov and Litvinchuk, 2007: fig. 13), and the extinct *Koalliella* (Estes, 1981) in: (1) having the portion of the neural arch dorsal to the postzygapophyses representing one-third of the vertebra height and (2) having the anterior and ventral crests forming an asymmetrical rhomboid structure with two large subcentral foramina. However, UM-DAM4-1 (and "Salamandridé G) differs from *Euproctus* in having a thinner posterior region of the centru, (Macaluso *et al*., 2023: fig. 11A). UM-DAM4-1 also seems to differ from *Calotriton*, *Ommatotriton* and *Lissotriton* in having a thicker dorsal portion of the neural crest (Ratnikov and Litvinchuk, 2007; Macaluso *et al*., 2023). This osteological character has been used to identify vertebra of the extinct *Koalliella* (Estes, 1981; Macaluso, pers. com. 2025). However, UM-DAM4-1 is too poorly preserved to confirm the neural crest bears a dorsal thickening (as seen in the modern *Salamandrina*) and cannot be assigned to *Koalliella*. Thus, we assign UM-DAM4-1 to an unnamed species of Oligocene pleurodeline, "Unnamed pleurodeline A".

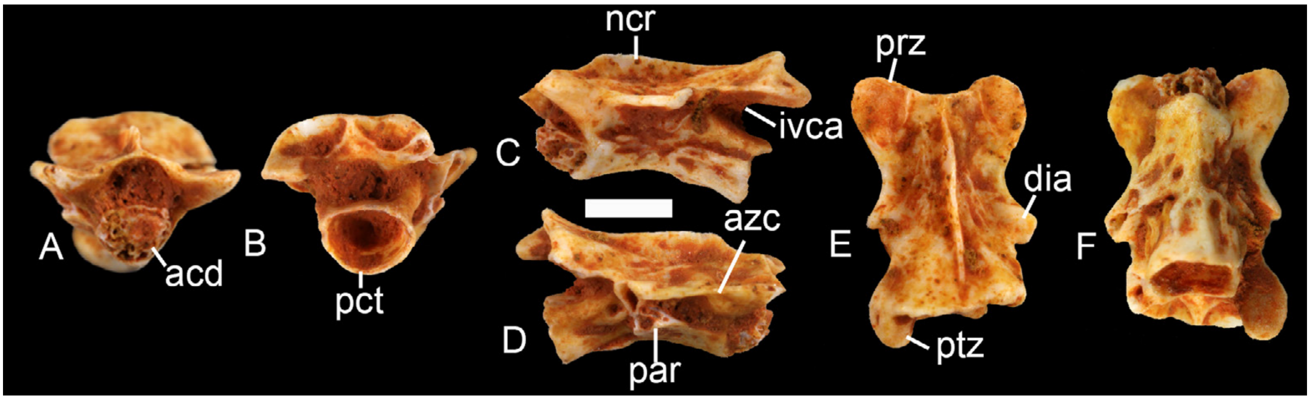

**Figure 3.** Oligocene indeterminate salamandrine of Dams. **A–F,** UM-DAM4-2, trunk vertebra of an indeterminate salamandrine in A, anterior, B, posterior, C, left lateral, D, right lateral, E, dorsal and F, ventral views. Scale bar equals 1 mm. Abbreviations: acd, anterior condyle; azc, anterior zygapophyseal crest; dia, diapophysis; ivca, incisura vertebralis caudalis; ncr, neural crest; par, parapophysis; pct, posterior cotyle; ptz, postzygapophysis; prz, prezygapophysis.

Unnamed pleurodeline B

Fig. 4F–J

**Referred specimen**: UM-DAM4-4, one trunk vertebra.

**Description:** UM-DAM4-4 is a small trunk vertebra (1 mm; Fig. 4F–J). The centrum is missing its posterior cotyle and the anterior condyle is broken off, showing its hollow condition. It indicates an opisthocoelous condition (Fig. 4F). The neural canal is wider and higher than the circular anterior condyle (Fig. 4F). The vertebra is not flattened dorsoventrally (neural arch portion dorsal to the postzygapophyses represents one-third of the vertebra height; Fig. 4G, H). In dorsal view, the anterior margin of the neural arch is straight, but the anterior condyle is still visible (Fig. 4I). The prezygapophyses are slightly expanded laterally (Fig. 4I). A thin and moderately developed neural crest is present (Fig. 4I). It extends posteriorly into a small neural spine (Fig. 4I). Both anterior and posterior zygapophyseal crests are present (Fig. 4G, H). The anterior ventral crest extends from the parapophyses to the dorsal surface of the anterior cotyle (Fig. 4G). Both diapophysis and parapophysis are distinguishable, separated by a bony lamina (Fig. 4F). Several foramina open in the lateral surface of the vertebra (Fig. 4G, H). In ventral view, the anterior ventral crests are developed (Fig. 4J).

**Attribution**: UM-DAM4-4 is assigned to the Pleurodelinae based on the following features: (1) bicipital transverse processes and opisthocoelous centrum (Salamandridae) and (2) marked anterior zygapophyseal crest. It differs from UM-DAM4-1 in having a lower and narrower neural crest and thus represents a second Oligocene pleurodeline in Dams. UM-DAM4-4 is reminiscent of extant small pleurodeline genera, like *Euproctus*, *Ichthyosaura*, *Ommatotriton* and *Lissotriton* (Ratnikov and Litvinchuk, 2007; Macaluso *et al*., 2023). However, the specimen is too poorly preserved for any assignment below the family level and is referred as "Unnamed pleurodeline B".

Anura Duméril, 1805

Pelobatidae Bonaparte, 1850

Unnamed pelobatid A

Fig. 5A–F

**Referred specimens**: UM-DAM1-335, one right maxilla; UM-DAM2-25, one frontoparietal; UM-DAM2-26, one sacral vertebra.

### Description

**Maxilla**: UM-DAM1-335 is a right maxilla missing the posterior and anteriormost regions (Fig. 5A–B). The labial surface is covered by an ornamentation made of pits and ridges (Fig. 5A). The pars facialis is high throughout the entire preserved length of the maxilla, with two peaks, the processus frontalis (anteriorly) and the processus zygomaticomaxillaris (posteriorly; Fig. 5A, B). On the lingual surface, the lamina horizontalis is slightly expanded dorsoventrally and flattened (i.e., not projecting lingually; Fig. 5B) and narrows posteriorly. The posterior region of the lamina horizontalis extends into a small processus pterygoideus (Fig. 5B). Anteriorly, the processus palatinus is broken at its base, exposing the end of the palatoquadrate groove (Fig. 5B). The tooth row does not preserve any intact teeth (Fig. 5B).

**Frontoparietal**: UM-DAM2-25 is a left frontoparietal (Fig. 5C, D). The dorsal surface bears an ornamented table consisting of pits and ridges (Fig. 5C) similar to the ornamentation recovered in UM-DAM1-335 (Fig. 5A). In ventral view, the base of the pars contacta is preserved along the entire length of the specimen (Fig. 5D). A laterally expanded tectum supraorbitale is present (Fig. 5D).

**Sacral vertebra**: UM-DAM2-26 is a sacral vertebra missing most of its sacral apophyses (Fig. 5E, F). The centrum bears an anterior cotyle and a posterior condyle (although the latter is poorly preserved; Fig. 5F). The prezygapophyses are small and extend laterally (Fig. 5E). The sacral apophyses are expanded

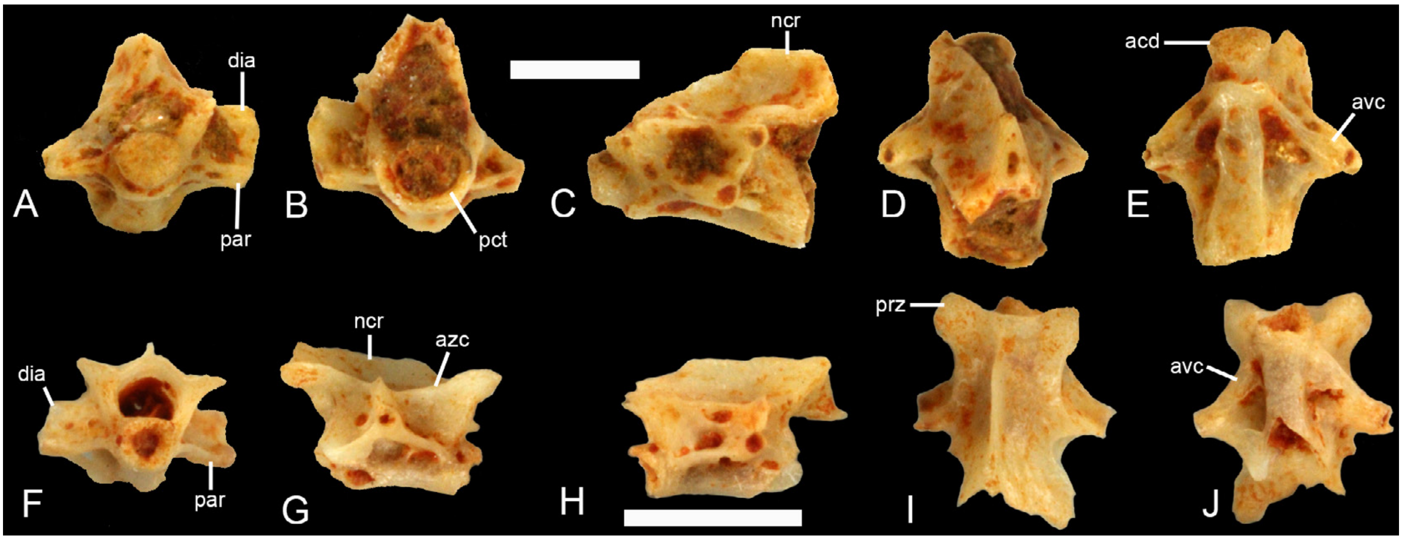

**Figure 4.** Oligocene newts (Pleurodelinae, Salamandridae) of Dams. **A–E**, UM-DAM4-1, trunk vertebra of the unnamed pleurodeline A ("Salamandridé G") in A, anterior, B, posterior, C, left lateral, D, dorsal and E, ventral views; **F–J**, UM-DAM4-3, trunk vertebra the unnamed pleurodeline B. in F, anterior, G, right lateral, H, left lateral, I dorsal, and J, ventral views. Images at different magnifications; see corresponding 1 mm scale bars. Abbreviations: acd, anterior condyle; avc, anterior ventral crest; azc, anterior zygapophyseal crest; dia, diapophysis; ncr, neural crest; par, parapophysis; pct, posterior cotyle; prz, prezygapophysis.

anteriorly and posteriorly, measuring twice the length of the centrum (Fig. 5F).

**Attribution**: The maxilla UM-DAM1-335 and frontoparietal UM-DAM2-25 are associated on the basis of a similar ornamentation made of pits and ridge (Fig. 5A, C). Within the Eocene of Western Europe, two anuran taxa are known to exhibit such ornamentation: *Thaumastosaurus* (Pyxicephalidae; Lemierre *et al*., 2021) and *Eopelobates* (Pelobatidae; Rage, 2006; 2016). UM-DAM1-335 differs from maxillae assigned to *Thaumastosaurus* in (1) lacking a smooth dorsal projection on its processus zygomaticomaxillaris and (2) having a lamina horizontalis not projecting lingually. UM-DAM2-25 differs from frontoparietals assigned to *Thaumastosaurus* in having a more developed tectum supraorbitale (Lemierre *et al*., 2021). Instead, both resemble isolate maxillae and frontoparietals assigned to Pelobatidae (Roček *et al*., 2014) on the basis of (1) laterally expanded tectum supraorbitale (UM-DAM2-25); and (2) lamina horizontalis not projecting lingually (UM-DAM1-335). The sacral vertebra UM-DAM2-26 is also referred to Pelobatidae in (1) having sacral apophyses anteriorly and posteriorly expanded; and (2) prezygapophyses short and extending laterally (Rage, 2016: fig. 2: 8). Within the known pelobatids from the Paleogene of Europe, only *Eopelobates* has ever been reported from the Eocene, *Pelobates* first appearing during the Oligocene (where it co-exists with *Eopelobates*; Roček *et al*., 2014). However, differences between the two genera are based on the squamosal/frontoparietal articulation, not preserved here. Thus, we assign all Eocene specimens from Dams to an indeterminate pelobatid, here informally called “Unnamed pelobatid A”.

Unnamed pelobatid B

Fig. 5G–L

**Referred material**: UM-DAM3-717, one presacral vertebra; UM-DAM4-5, a right frontoparietal; UM-DAM4-6, an indeterminate skull fragment.

### Description

**Frontoparietal**: UM-DAM4-5 is a right frontoparietal missing most of its anterior and posterior regions (Fig. 5G). The medial margin shows both left and right frontoparietals were fused (at least at midlength; Fig. 5H). The dorsal surface of the frontoparietal is covered with pits and ridges ornamentation (like in the cf. *Eopelobates*; Fig. 5G). The pars contacta is only preserved as a thin ridge delimiting the large tectum supraorbitale (Fig. 5H). The latter widens posteriorly into a posterolateral expansion (Fig. 5G, H). The incrassatio frontoparietalis is preserved as a large shallow imprint (Fig. 5H).

**Presacral vertebra**: UM-DAM3-717 is a presacral vertebra missing most of its transverse processes and the right postzygapophysis (Fig. 5I–L). The centrum is procelous and cylindrical shaped (Fig. 5I, J, L). The neural arch is flattened dorsoventrally (Fig. 5I–K). The prezygapophyses are small and oriented laterally (Fig. 5K). The neural spine is low and extends posteriorly into a well-developed posterior process (Fig. 5K). The transverse processes are curved dorsally and oriented laterally (Fig. I, J). Thus, the vertebra likely came from the middle portion of the vertebral column.

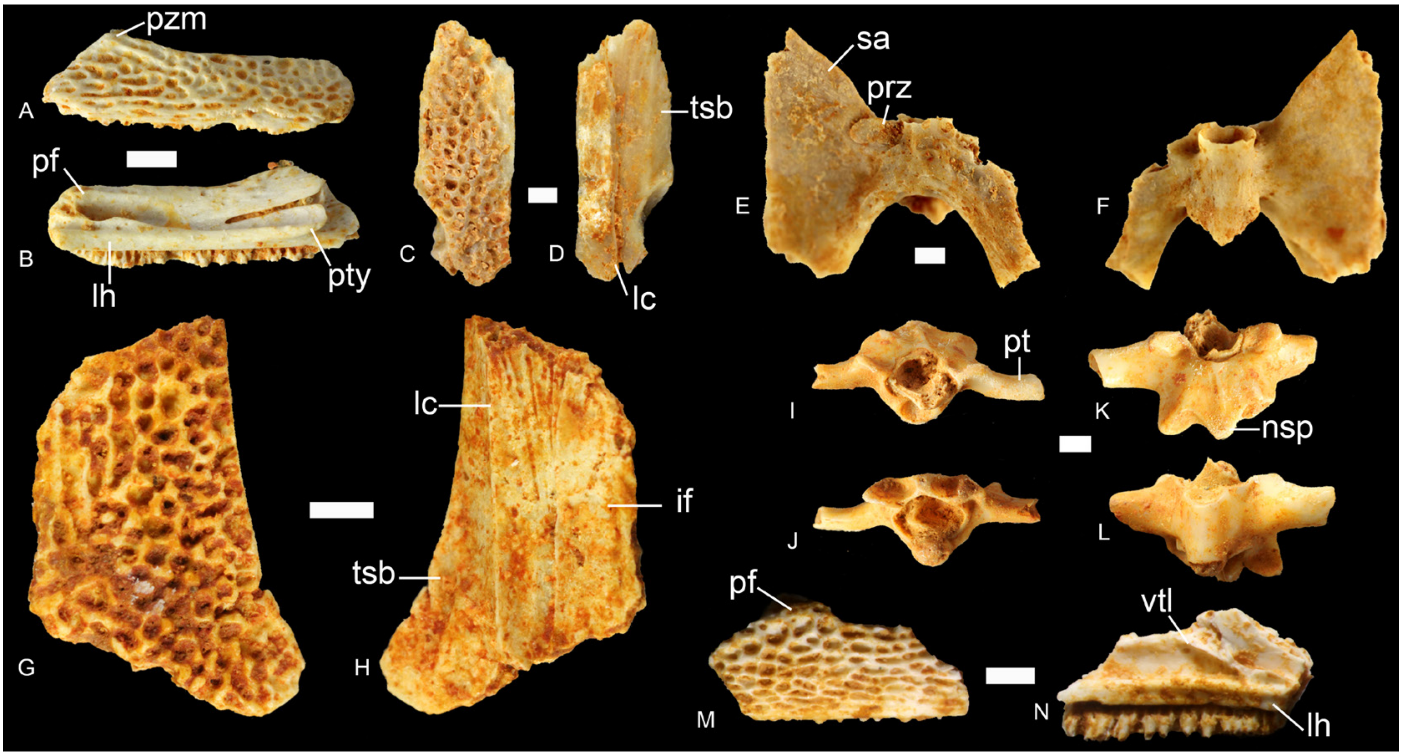

**Figure 5.** Anurans of Dams. **A–B**, UM-DAM1-335, right maxilla of the unnamed pelobatid A in A, labial and B, lingual views; **C–D**, UM-DAM2-25, frontoparietal of unnamed pelobatid A in C, dorsal and D, ventral views; **E–F**, UM-DAM2-26, sacral vertebra of unnamed pelobatid A in E, dorsal and F, ventral views; **G–H**, UM-DAM4-5, frontoparietals of an unnamed pelobatid B in G, dorsal and H, ventral views; **I–L**, UM-DAM3-717, presacral vertebra of an unnamed pelobatid in I, anterior, J, posterior, K, dorsal and L, ventral views; **M–N**, UM-DAM1-336, left maxilla of *Thaumastosaurus* sp. in M, labial and N, lingual views. Images at different magnification; see corresponding 1 mm scale bars. Abbreviations: if, incrassation frontoparietalis; lc, pars contacta; lh, lamina horizontalis; nsp, neural spine; pf, processus frontalis; pt, processus transverse; pty, processsus pterygoideus; pzm, processus zygomaticomaxillary; prz, prezygapophysis; sa, sacral apophysis; tsb, tectum supraorbitale; vtl, vertical lamina.

**Attribution:** The presence of (1) an ornamentation made of pits and ridges; (2) a large incrassatio frontoparietalis and (3) well-developed tectum supraorbitale warrants an assignment of the frontoparietal UM-DAM4-5 to the Pelobatidae. A small fragment of an undetermined cranial element (UM-DAM4-6) exhibits the same ornamentation and is referred to the same taxon as the frontoparietal. The presacral vertebra UM-DAM3-717 is assigned to the Pelobatidae based on (1) the procelous and cylindrical centrum and (2) the well-developed posterior projection of the neural spine (Bailon, 1999). All three specimens are assigned to the same taxon as we have no indication that two taxa of pelobatid were present in the Oligocene of Dams. UM-DAM4-5 differs from UM-DAM2-25 in (1) larger size and (2) having a posterolateral expansion of the tectum supraorbitale. Thus, the pelobatid from the Oligocene of Dams is a distinct taxon from the unnamed pelobatid A of its Eocene layers. Because both *Eopelobates* and *Pelobates* co-exist in the Oligocene, both exhibit an ornamentation made of pits and ridges and we are lacking the frontoparietal/squamosal articulation, our Oligocene specimens are assigned to an indeterminate pelobatid, informally called “unnamed pelobatid B”.

Neobatrachia Reig, 1959

Ranoidea Rafinesque, 1814

Natatanura Frost, Grant, Faivovich, Haas, Haddad, De Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Blotto, Moler, Drewes, Nussbaum, Lynch, Green, and Wheeler, 2006

Pyxicephaloidea Tschudi, 1838 [Lemierre and Laurin, 2021]

Pyxicephalidae Tschudi, 1838 [Lemierre and Laurin, 2021]

*Thaumastosaurus* De Stefano, 1903

*Thaumastosaurus* sp.

Fig. 5M–N

**Referred specimens**: UM-DAM1-336, one left maxilla.

**Description**: UM-DAM1-336 represents the anterior portion of a left maxilla (Fig. 5M, N). The entire labial surface is covered in pit and ridge ornamentation (Fig. 5M). The lingual surface bears a lamina horizontalis slightly expanded dorsoventrally (Fig. 5N). The lamina slightly projects lingually along its posterior region (Fig. 5N). The lingual surface of the processus frontalis bears a broken and almost vertical lamina (Fig. 5N).

**Attribution**: UM-DAM1-336 differs from UM-DAM1-335 (maxilla of cf. *Eopelobates*) in having an almost vertical lamina on the lingual surface of the processus frontalis (Fig. 5N). The presence of this lamina has been used a diagnostic character for the genus *Thaumastosaurus* (Roček and Lamaud, 1995; Lemierre *et al*., 2021; Georgalis *et al*., 2023). It is not currently possible to separate species of *Thaumastosaurus* on their maxillae, hence UM-DAM1-335 is assigned to *Thaumastosaurus* sp.

## DISCUSSION

### Lissamphibians diversity in Dams

Even though only thirteen specimens from Dams belong to lissamphibians, they represent eight distinct taxa (Table 1). Two distinct assemblages are identified, an Eocene one (six specimens for four species) and an Oligocene one (seven specimens for four species). Both assemblages are dominated by salamanders (five species out of eight; Table 1), likely a taphonomic bias rather than a reflection of the palaeodiversity (karstic infillings rarely preserved amphibian specimens; Rage, 2012, 2016).

Lissamphibians have been described from Late Eocene and Oligocene localities of the Quercy area (for review see Rage, 2006). However, detailed work on the lissamphibians assemblages is available for a very limited number of localities (Escamps, Sainte-Néboule, Brétou for the Late Eocene; Le Gargouillas and Valbro for the Oligocene; Rage, 1988; Rage and Vergnaud-Grazzini, 1978; Augé and Rage, 1995; Rage and Augé, 2015) and illustrations are scarce.

Based on the literature (following reviews of Duffaud, 2000; Rage, 2006, 2016) and on the present study, anurans of the MP19 (Late Eocene) are represented by the following taxa at the generic level: (1) an indeterminate alytid; (2) cf. *Pelodytes*; (3) an indeterminate pelobatid; (4) the ranoid *Thaumastosaurus* (represent by several species); (5) an indeterminate mid-size ranoid (could represent more than one taxon); (6) an indeterminate large size ranoid. For salamanders, Five taxa are identified: (1) *Megalotriton* (Salamandrinae); (2) “unnamed salamandrine A” (Salamandrinae; identified as “Salamandridé C” in previous studies); (3) “unnamed salamandrine B” (identified for the first time in this study); (4) “unnamed pleurodeline A” (Pleurodelinae, identified as “Salamandridé G” in previous studies), and (5) the strange *Phosphotriton* (?Salamandridae, likely MP19; following Tissier *et al*., 2016; Lemierre *et al*., 2021) . Thus, at least eleven lissamphibians taxa (at the generic level) are identified within MP19 localities in the Quercy.

In the Quercy area, the only locality coeval with the Eocene assemblage of Dams (MP19) with lissamphibians adequately described and figured is Escamps (see Duffaud, 2000 and Rage, 2016 for description and identification). In this locality, at least seven taxa, at the generic level, are identified (Table 1): (1) an indeterminate alytid; (2) an indeterminate pelobatid; (3) an indeterminate mid-size ranoid; (4) an indeterminate large size ranoid; (5) *Thaumastosaurus* (Pyxicephalidae, Ranoidea); (6) *Megalotriton*, and (7) “unnamed salamandrine A”. Three taxa from Escamps are also recovered in Dams; (1), “unnamed salamandrine A”; (2) *Thaumastosaurus*; and (3) an unnamed pelobatid. Notably absent from Dams is the large salamandrine *Megalotriton*, recovered in Escamps and most MP19 localities (according to Duffaud, 2000) and the number of anuran genera in Dams is poorer than in Escamps (two genera vs. five in Escamps; Rage, 2016). This smaller lissamphibian diversity is likely linked to the small number of specimens collected (six) in Dams. However, despite this small number of specimens, we identify a new Eocene taxon, an unnamed salamandrine (“unnamed salamandrine B”), increasing to eleven the number of lissamphibian taxa recorded in the MP19 level in Quercy.

Based on the literature (Rage, 2006; Rage, 2016) and this study, we consider anurans of the MP 22 to be represented by the following taxa (at the generic level): (1, 2) two indeterminate alytids; (3) an indeterminate pelobatid and (4) an indeterminate ranoid. Salamanders are represented (at the generic level) by: (1) cf. *Megalotriton* sp. (Salamandrinae); (2) *Salamandra* (Salamandrinae); (3) “unnamed pleurodeline A”, and (4) “unnamed pleurodeline B” (identified for the first time in this study). Thus, eight lissamphibian taxa are identified within MP22 Quercy localities.

Lissamphibians have been described and illustrated from

**Table 1.** List of lissamphibians species identified in Dams and coeval localities of Escamps (Late Eocene, MP19) and Valbro (Early Oligocene, MP22).

| | **Eocene DAM1+DAM2 (MP19)** | **Oligocene DAM4 (MP22)** | **Escamps MP19** | **Valbro MP22** |
|---|---|---|---|---|
| **Urodela** | | | | |
| **Salamandridae** | | | | |
| **Pleurodelinae** | | | | |
| | - | Unnamed pleurodeline A | - | - |
| | - | Unnamed pleurodeline B | - | - |
| **Salamandrinae** | | | | |
| | Unnamed salamandrine A | *Salamandra sansaniensis* | *Megalotriton fiholi* | cf. *Megalotriton* |
| | Unnamed salamandrine B | Salamandrinae indet. | "Salamandridé C" / Unnamed salamandrine A | *Salamandra* sp. |
| **Anura** | | | | |
| **Alytidae** | - | - | Indeterminate alytid | Indeterminate "*Discoglossus* " |
| **Pelobatidae** | Unnamed pelobatid A | Unnamed pelobatid B | Indeterminate pelobatid | Indeterminate pelobatid |
| **Neobatrachia** | | | Indeterminate mid-sized ranoid | - |
| **Ranoidea** | | | Indeterminate large-sized ranoid | - |
| **Pyxicephalidae** | *Thaumastosaurus* sp. | | *Thaumastosaurus* sp. | - |

a single locality in the Quercy area for the Early Oligocene, Valbro (Rage and Augé, 2015). The locality of Valbro has yielded four lissamphibians (Table 1): (1) an indeterminate alytid ("*Discoglossus*"); (2) an indeterminate pelobatid; (3) cf. *Megalotriton*, and (4) *Salamandra* (not identified at the species level, but consistent with *S. sansaniensis*; Rage and Augé, 2015). Two of the Valbro taxa are also identified in the Oligocene assemblage of Dams: (1) an indeterminate pelobatid and (2) *Salamandra sansasniensis*. However, salamanders in Dams are more diverse (at the generic level) with three taxa (vs. two in Valbro), including two pleurodeline (absent at Valbro). As for the Eocene assemblage, despite the small number of lissamphibians specimens (seven), we identified a new taxon for the Quercy, an unnamed pleurodeline ("unnamed pleurodeline B") and increase the taxonomic diversity (at the generic level) of the MP22 of the Quercy to eight taxa.

Thus, among the eight amphibians present in Dams, we identify two new taxa for the Quercy Phosphorites, an unnamed Eocene salamandrine and an unnamed Oligocene pleurodeline. The diversity of the Eocene assemblage documented from Dams is poorer than its coeval localities in the Quercy most probably due to the small number of specimens available. With four species, the diversity of the Oligocene assemblage of Dams is similar to that of its coeval locality Valbro.

## Evolution around the Eocene-Oligocene transition

Based on published and unpublished data, several authors have considered lissamphibians to undergo a major extinction event at the "Grande Coupure" in the Quercy and Western Europe, with the extinction of most anurans (Rage, 2006, 20016; Rage and Roček, 2003; Vasilyan, 2018). During the Eocene-Oligocene transition, two anuran families, Pelodytidae and Pyxicephalidae, disappear from the Quercy and Western Europe fossil record (Rage, 2012; 2016; Pelodytidae reappear in Europe during the Miocene, Sanchíz, 1998). However, in the absence of generalized comparisons between Eocene and Oligocene anurans (in families surviving the "Grande Coupure"), it is difficult to assess how affected they actually were at the transition. Yet, based on the minimum number of taxa present in the Late Eocene and Early Oligocene (see above), anuran diversity decreases by a third during the "Grande Coupure", suggesting an effect of the environmental changes of the Eocene/Oligocene transition on that group.

In Dams, we did not identify any pelodytids, but pyxicephalids, with *Thaumastosaurus*, are present in the Eocene assemblage (Table 1). No pyxicephalids are present in the Oligocene assemblage of Dams, in coherence with the family's extinction at the Eocene/Oligocene transition. The presence of distinct pelobatid taxa between the Eocene and Oligocene assemblages in Dams suggests a complete turnover within the family in the Quercy, but no conclusion can be drawn based on 13 specimens only, and more material and a complete revision of the cranial and postcranial elements assigned to the family is required to adequately discuss the evolution of diversity.

Salamanders are represented in the Quercy by a single family, Salamandridae, and both of its subfamilies, Pleurodelinae and Salamandrinae, are present in the Eocene and Oligocene of the

Quercy. A slight decrease in taxonomic diversity is recorded at the Eocene-Oligocene transition (five vs. four), but members of both subfamilies survive. Two salamander taxa survive the "Grande Coupure".

The major extinction recorded among lissamphibians has often been lumped with the extinction recorded in Squamata (in which >75% of taxa disappeared; Rage, 2006, 2012) and rarely discussed beyond systematics (Rage, 1984, 2006. 2012). Lissamphibians can be both specialized to a given habitat or more generalists (Duellman and Trueb, 1994), but they are all very sensitive to temperature and humidity variations (Duellman and Trueb, 1994), and the Eocene-Oligocene transition marks a period of significant decrease in temperature, sea level, and precipitation (Mostbrugger *et al*. 2005; Coxal *et al*. 2007; Miller *et al.* 2020; Westerhold *et al*. 2020), and a concurrent increase in seasonality in Europe during the Oligocene (Mostbrugger *et al*. 2005; Pound *et al*. 2017; Toumoulin *et al*. 2022). An extinction event of lissamphibian taxa at the Eocene/Oligocene transition is most likely and would affect: (1) taxa specific to more forested environment and (2) taxa adapted to warm and humid environments (as hypothesized by Rage, 2016 and Vasilyan, 2018). Thus, the Early Oligocene fauna is expected to be composed of more generalist taxa, in addition to newcomers adapted to a more arid and cooler environment (Rage, 2016).

Larger scale comparison between the Quercy area and the rest of Western Europe is difficult due to the very limited number of lissamphibians described from Early Oligocene localities and the absence of recent comprehensive reviews of European lissamphibians (Roček and Rage, 2003). As an example, Alytids are known in most Upper Eocene and Lower Oligocene localities in Western Europe (Roček and Rage, 2003; Roček, 2013) but have been identified at various taxonomic level (family, genus, species) and few comparisons between localities exist (Roček and Rage, 2003). It should be noted that a main difference between the Quercy and other localities can be observed, the absence of obligate aquatic lissamphibians taxa. As such, cryptobranchidas, palaeobatrachids and proteids are not recorded from the Quercy area, while they are recovered across Western Europe during the Eocene and Oligocene (Roček and Rage, 2003). One possible comparison is that most Lower Oligocene localities from Western and Central Europe have a poor lissamphibian diversity, with one to four taxa (Lemierre *et al*., 2022; Roček and Rage, 2003; Sanchíz *et al*., 1993).

In Central Europe, lissamphibians from five localities from the north-western side of the Transylvanian Basin, bordering the Eocene-Oligocene transition, have recently been described (Venczel *et al*., 2024). Two localities from the Upper Eocene (Bociu and Trezena) have yielded four anurans: (1), *Latonia* sp. (Discoglossidae); (2), an indeterminate palaeobatrachid; (3), an indeterminate pelobatid and (4) *Pelophylax* sp. (Ranoidea, Ranidae). No salamanders are present in these Eocene localities. The three Lower Oligocene localities (Suceag 1, Cetățuia Hill and Cluj-Napoca) have also yielded four taxa, one salamander and three anurans: (1) *Mioproteus gardneri* (Proteidae); (2) *Latonia* sp. (Discoglossidae); (3) *Albionobatrachs oligocenicus* (Palaeobatrachidae), and (4) *Pelophylax* sp. (Ranoidea, Ranidae). These two lissamphibian assemblages are less diverse than their Quercy counterpart (half of the Quercy diversity). Between the two assemblages from Central Europe, a minor turnover is recorded, with only a single taxon disappearing (indeterminate pelobatid) and one appearing (*Mioproteus*), suggesting different turnover rate between Western and Central Europe.

## CONCLUSION

The lissamphibian fossils retrieved from the karstic infillings of Dams are not numerous (13 specimens in total) but they record a non-negligible diversity and document new taxa in the Quercy area. At least eight distinct species, four found in the Eocene assemblage and four in the Oligocene assemblage are identified. The diversity observed in Dams, despite the small number of specimens found, highlights the rich diversity of lissamphibians in the Quercy area during the Eocene-Oligocene. The late Eocene assemblage is comprised of two species of salamandrine (Unnamed salamandrine A and B), one indeterminate species of pelobatid (Unnamed pelobatid A) and one indeterminate species of *Thaumastosaurus* (Ranoidea, Pyxicephalidae). Within this assemblage, the unnamed salamandrine B represents a third taxa for this subfamily in the Quercy (for the Late Eocene). The early Oligocene assemblage is comprised of the salamandrine *Salamandra sansaniensis*, two unnamed species of pleurodelines (Unnamed pleurodeline A and B) and one indeterminate species of pelobatid (Unnamed pelobatid B). One of the unnamed species of pleurodeline (unnamed pleurodeline B would represent a second taxa from this subfamily in the Quercy (for the Early Oligocene). Review of the known published lissamphibians from Upper Eocene (MP19) and Lower Oligocene (MP22) localities identify eleven (for MP19) and eight (MP22) taxa in the Quercy area. Comparisons between both assemblages are difficult due to the absence of generalized comparisons beyond the regional scale, but two Eocene anuran families, Pelodytidae and Pyxicephalidae, seem to go extinct at the Eocene-Oligocene transition. A major lissamphibian fauna turnover seems to be observed in the Quercy fossil record at the Eocene-Oligocene transition. Additional material and local scale revisions are needed before going further into discussing diversity dynamics of the group. Yet, an impact of the major environmental changes that occurred at this period at the European scale is expected on lissamphibians, highly sensitive to temperature and humidity variations.

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