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A new Late Miocene small vertebrate assemblage from the Ouarzazate Basin (High Atlas, Morocco) and its biochronological and paleoenvironmental significance

Pedro Piñero[1,2], Jordi Agustí[2,3,4], Hugues-Alexandre Blain[3,4], Ángel Blanco-Lapaz[5,6], Eliseo Tesón[7], Antonio Teixell[8], Marc Furió[2,8]

1 *Departament de Botànica i Geologia, Universitat de València, Doctor Moliner 50, 46100 Burjassot, Spain*
2 *Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain*
3 *IPHES-CERCA, Institut Català de Paleoecologia Humana i Evolució Social, Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain*
4 *Departament d'Història i Història de l'Art, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain*
5 *Senckenberg Centre for Human Evolution and Paleoenvironment (SHEP), Hölderlinstrasse, 12 72074 Tübingen, Germany*
6 *Institute for Archaeological Sciences, University of Tübingen, Hölderlinstrasse 12, 72074 Tübingen, Germany*
7 *Ecopetrol S.A., Bogotá, Colombia*
8 *Departament de Geologia, Universitat Autònoma de Barcelona, 08193, Bellaterra, Spain*

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Corresponding author: Marc Furió (marc.furio@uab.cat))

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Abstract

The Ouarzazate Basin is located between the southern flank of the Central High Atlas and the Anti-Atlas mountains (in Morocco). The Neogene is primarily represented by the Aït Ouglif and Aït Kandoula alluvial formations, which are exposed in the Amekchoud section. Magnetostratigraphic data indicate a Middle to Late Miocene age for this sequence, from the upper Langhian to the Messinian. Despite extensive sampling, significant paleontological results were only obtained at level PAM 207, situated 773 m above the base of the Aït Kandoula formation. This level, characterized by reversed polarity, yielded a microvertebrate assemblage preliminarily described by Tesón et al. (2010). In this work we present a revised study of the small vertebrates from PAM 207, providing updated information on its faunal composition as well as new insights into the biostratigraphy and paleoenvironment of the locality. The assemblage includes fishes, amphibians, reptiles, insectivores, and rodents. Based on the rodent association, PAM 207 is slightly younger than Guefait 1 (Morocco) and close in age to Sidi Salem (Algeria), representing one of the oldest early Turolian localities in North Africa. It postdates Tafna 2 (9.1–8.7 Ma) and predates Amama 2 (7.7 Ma), supporting its correlation with chron C4r (8.77–8.12 Ma). Paleoenvironmental evidence suggests temperate freshwater habitats within an open landscape with a certain degree of vegetative cover, under relatively arid conditions. Overall, PAM 207 provides new evidence that contributes to the establishment of a chronologically constrained Late Miocene biochronological scheme for North Africa and enhances our understanding of paleoenvironments during this interval.

Key Words

Anura, biostratigraphy, Cypriniformes, Eulipotyphla, paleoecology, Rodentia, Squamata

Introduction

Despite the relatively rich late Neogene record of fossil small vertebrates in North Africa, few localities are supported by robust chronological constraints based on paleomagnetism or numerical dating (Werdelin 2010; Duval et al. 2025). Consequently, dating remains poor and often controversial, relying mainly on biochronological correlations with faunas from outside the continent. While several calibrated biochronological schemes for the late Cenozoic have been developed in western Europe, particularly in Spain (e.g., Agustí et al. 2015; Piñero et al. 2018), North Africa is still far from establishing a chronologically constrained framework. Although biostratigraphic approaches and syntheses based on small faunas have been conducted (Stoetzel 2013; Zouhri et al. 2017; Zouhri and Amane 2022), further independent dating efforts are required to achieve a robust biochronological framework. Late Miocene microvertebrate sites in North Africa calibrated by paleomagnetic or radiometric data include Bou Hanifia 5 (Sen 1986), the Afoud section (Benammi et al. 1996), Oued Tabia (Benammi 1997), Tafna 2 (Mahboubi et al. 2015), Oued Zra (Jaeger 1977; Harland et al. 1982), Amama 2 (Coiffait-Martin 1991; Mahboubi and Benammi 2020), and PAM 207 (Tesón et al. 2010), among others. In the present study, we focus on the latter site.

The Ouarzazate Basin, located in front of the High Atlas of Morocco, is filled mainly by the Aït Ouglif and Aït Kandoula alluvial formations, both exposed in the Amekchoud section (Tesón et al. 2010). A previous magnetostratigraphic study indicated a Middle to Late Miocene age for the sequence, spanning from the upper Langhian to the Messinian. Despite extensive paleontological sampling throughout the succession, significant results were only obtained from level PAM 207, situated 773 m above the base of the section near the village of Amekchoud (Ouarzazate Province, Morocco). The location coordinates are 31°13'19"N, 6°36'44"W (Fig. 1A). According to Tesón et al. (2010), this level, which has a reversed polarity, yielded a significant assemblage of microvertebrates. These authors presented a preliminary list of small mammals, including the insectivore Oligosoricini indet., the rodents *Myocricetodon* cf. *afoudensis*, *Zramys* cf. *hammamai*, *Paraethomys* cf. *miocaenicus*, and *Africanomys* sp., as well as the anuran *Latoglossus* sp. However, they did not provide a complete description or discussion, as they did not include either fish or herpetofauna, which highlighs the need for a thorough taxonomic revision.

While the Late Miocene small mammal record of North Africa is relatively well known (Stoetzel 2013, and references therein), the fossil herpetofauna has been comparatively poorly studied. Amphibians and squamate reptiles are reported from only a few localities, such as the early Late Miocene (Vallesian) sites of Oued Zra and Khendek-el-Ouaich (Hossini 2000, 2002), and Guefaït 1 (Blain et al. 2013). Moroccan ichthyofaunas are well-documented for the Mesozoic, forming an important component of marine vertebrate assemblages (Khalloufi et al. 2017). However, the study of freshwater fish remains from the Late Miocene remains scarce. Only two localities within the Aït Kandoula Formation have yielded fish remains, primarily teeth, namely Afoud 6 and Azaghar (Benammi et al. 1995). The study of PAM 207, which includes fishes, herpetofauna, and small mammals, provides an excellent opportunity to expand our knowledge of the different taxonomic groups of the Late Miocene in North Africa.

Here, we revise the small vertebrate collection to provide updated and expanded information on the taxonomic composition of the assemblage (fishes, amphibians, reptiles, and small mammals), including a comprehensive description and discussion of the taxa. This provides a solid basis for reassessing the age of the site and would contribute to tentatively establishing the chronological boundaries for the biozonation of North Africa. In addition, we offer new insights into the paleoenvironment of the locality.

Geological settings

The fossil material originates from the Ouarzazate Basin, a Cenozoic foreland basin located in front of the Atlas Mountains, where it constitutes a rather infrequent structure. The Ouarzazate Basin is a small, elongated basin approximately 145 km long, with a maximum width of 35 km and a depth of 800 m on its southern side, adjacent to the High Atlas front. It is bounded on its northern margin by a marginal thrust belt known as the Sub-Atlas Zone. This deformed zone separates the basin from the High Atlas, an overall E–W trending thrust and fold belt localized in the NW African plate. This mountain range was formed by the Cenozoic inversion of a Mesozoic transtensional rift (Arboleya et al. 2004, and references therein), and it is primarily composed of Paleozoic and Mesozoic rocks, with the latter predominantly of Jurassic age.

The sedimentary infill of the Ouarzazate Basin is dominated by Neogene alluvial fan to lacustrine sediments, occasionally covered by Quaternary pediments and terraces. The basin yields a section of more than 1000 m of fluvial-alluvial sediments. The most complete and best-exposed succession in the study area of Amekchoud is summarized in Tesón et al. (2010). The Aït Ouglif and Aït Kandoula Formations, well exposed in the Amekchoud area, are syntectonic formations that form the bulk of the infill of the Ouarzazate foreland basin. Magnetic stratigraphy and vertebrate fossil assemblages from the Late Miocene were used to date these formations (Tesón et al. 2010). According to the authors, these formations span from the Langhian to the Messinian, although the Aït Kandoula formation may reach the base of the Pliocene in the Aït Kandoula intramontane basin north of Ouarzazate (Benammi et al. 1996; El Harfi et al. 2001; Benvenuti et al. 2020; Mahboubi et al. 2022).

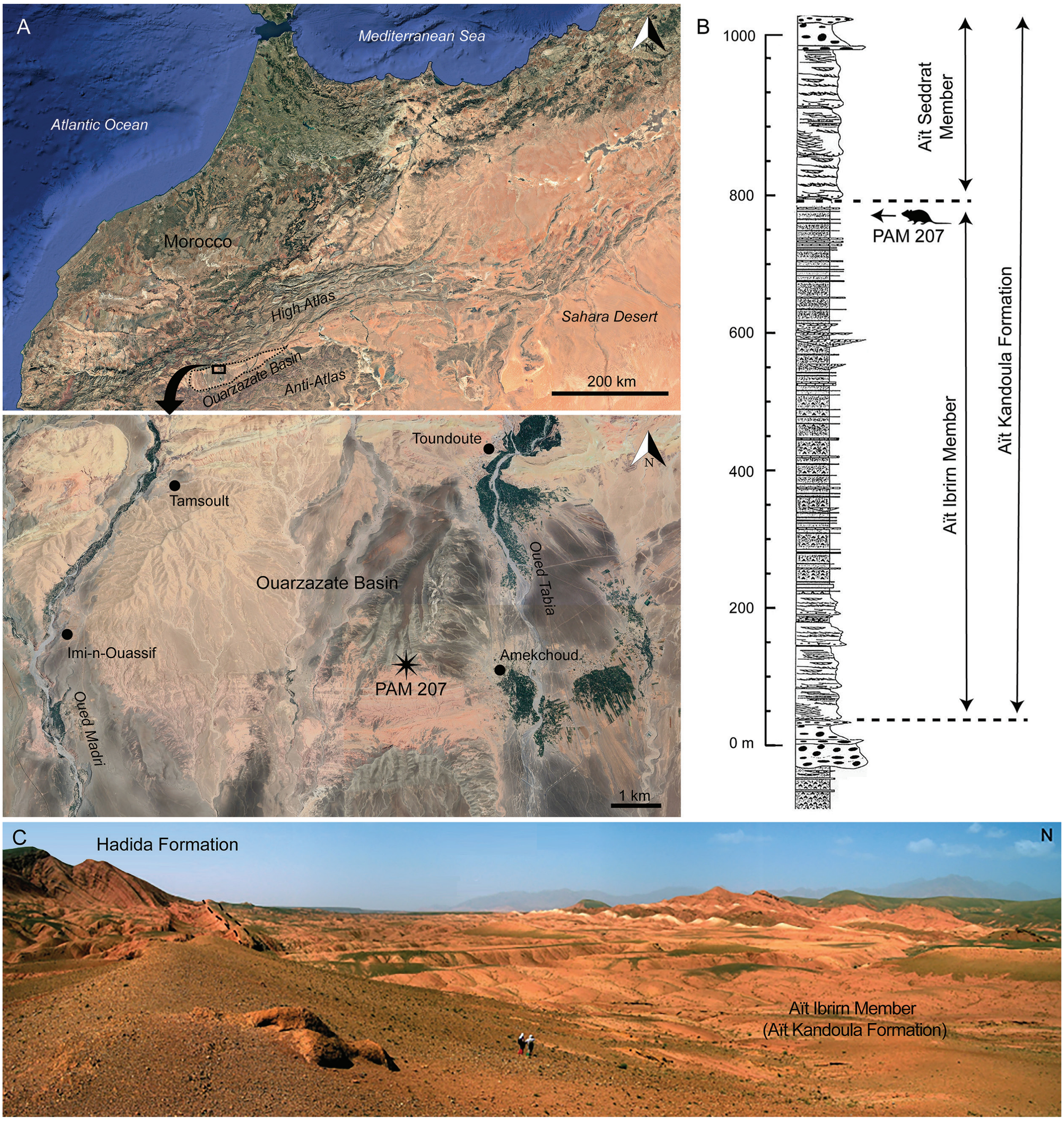

Figure 1. Geographic and stratigraphic context. **A.** Location of the PAM 207 site (source: Google Earth Pro); **B.** Stratigraphic log of the Amekchoud section with the position PAM 207 (modified from El Harfi 1994; Tesón et al. 2010); **C.** General view of the Tertiary succession in the Amekchoud area (Ouarzazate Basin). View from Amekchoud village looking west (taken from Tesón et al. 2010).

Level PAM 207 of the Aït Kandoula Formation yielded the small vertebrate fossils described in this study. This bed belongs to the Aït Ibrirn Member of the formation and is located 773 m above the base of the Aït Kandoula formation (Fig. 1B, C) (Tesón et al. 2010). The part of the Aït Ibrirn Member that includes PAM 207 is dominated by lacustrine carbonates, a sequence that yielded a reversed polarity, which was correlated with chron C4r (8.77–8.12 Ma) by Tesón et al. (2010).

The chronostratigraphic context of the mammal assemblages previously recovered from the Ait Kandoula Formation (Benammi et al. 1996; Benammi and Jaeger 2001; Benammi 2006; Tesón et al. 2010; Geraads et al. 2012; Zouhri et al. 2012; Cirilli et al. 2020) has been crucial for reconstructing a consistent evolution framework of the Ouarzazate Basin (Benvenuti et al. 2020).

Material and methods

In 2008, a field campaign focused on magnetostratigraphy and paleontology was carried out in the northern part of the Ouarzazate Basin, west of the village of Amekchoud. Micropaleontological sampling of the

Aït Kandoula Formation was conducted at four levels (PAM = 'Paleontological Assemblage Miocene'): PAM 135, PAM 141, PAM 207, and PAM 209, located at 503, 525, 773, and 790 m, respectively, above the base of the Amekchoud section. Despite extensive sampling and wet screen-washing of the retrieved sediments, only the level PAM 207 yielded significant results.

The fossil material collected from PAM 207 consists of 115 disarticulated elements of microvertebrates. The collection comprises 14 teeth and bones of fishes belonging to at least one taxon, 86 disarticulated cranial and postcranial bones of amphibians and squamate reptiles assigned to two taxa, and 15 identified small mammal teeth from five different taxa. These fossils are housed in the collections of the Institut Català de Paleontologia Miquel Crusafont (ICP; Sabadell, Barcelona, Spain).

All measurements are given in millimeters and were taken on the occlusal plane of the teeth using DinoCapture 2.0, based on photographs obtained with the Digital Microscope AM4115TL Dino-Lite Edge. The fish material was photographed using a Zeiss Stereo Discovery. V12 digital microscope (Tübingen, Germany). The amphibians and reptiles are illustrated by means of digital photographs, using a Digital Microscope AM7915MZTL Dino-Lite Edge, alongside the DinoCapture 2.0 software for photo-stacking. Small mammal teeth are illustrated with micrographs acquired via Environmental Scanning Electron Microscopy (ESEM) at the Servei de Recursos Científics i Tècnics, Universitat Rovira i Virgili (Tarragona). Upper teeth are indicated by capital letters, and lower teeth by lowercase letters. Therefore, incisors are indicated as I or i, and molars as M or m.

We described the fish material based on modern comparative specimens housed at the University of Tübingen. The systematic nomenclature generally follows Speybroeck et al. (2020) for extant herpetofaunal taxa. Osteological nomenclature mainly follows Roček (1994), Sanchiz (1998), and Blain et al. (2016a) for anurans, and Hoffstetter (1962), Augé (2005), and Barahona and Barbadillo (1997) for lizards. For the descriptions and measurements of Soricidae teeth, we followed Reumer (1984). The methodology of Mein and Freudenthal (1971) was applied to Myocricetodontinae teeth, while Muridae teeth were described and measured following Van de Weerd (1976) and Martín-Suárez and Freudenthal (1993), respectively. For Ctenodactylidae teeth, we followed Baskin (1996).

Systematic palaeontology

Class Actinopterygii Cope, 1887
Clade Teleosteomorpha Arratia, 2000
Order Cypriniformes Bleeker, 1859
Family Cyprinidae Rafinesque, 1815
Subfamily Cyprininae (Rafinesque, 1815) (sensu Yang et al., 2015)
Tribe Barbini Bleeker, 1859 (sensu Yang et al., 2015)
Genus *Luciobarbus* Heckel, 1843

Luciobarbus sp.

Fig. 2A, B

Material. Two pharyngeal teeth (IPS-PAM207-15, IPS-PAM207-16).

Description and remarks. Both pharyngeal teeth are elongate and twisted along their longitudinal axis. The tooth crown shows an anteriorly directed pointed hook.

The genus *Luciobarbus* (barbel) has pharyngeal teeth arranged in three rows, with the following formula: five teeth in the first row, three in the second, and two in the third. Similar to other Barbini genera, the teeth in the first row are larger than those in the other two rows. The two small pharyngeal teeth found belong to the third row. In both cases the tooth body is compressed at the foot-crown border, and the crown is slightly narrower than the base. The pharyngeal teeth are also characterized by the presence of a hook at the top of the grinding surface (Escala and Miranda 2002; Vasylan et al. 2019).

Several species belonging to the genus *Luciobarbus* are currently present in Morocco (*L. callensis*, *L. guercifensis*, *L. lanigarensis*, *L. maghrebensis*, *L. magniatlantis*, *L. nasus*, *L. pallaryi*, *L. rabatensis*, *L. yahyaouii*, and *L. zayanensis*) (Clavero et al. 2017). Due to the lack of a complete pharyngeal arch, classification at the species level is not possible for these remains.

Barbini indet.

Fig. 2C–E

Material. Three pharyngeal teeth (IPS-PAM207-17–IPS-PAM207-19).

Description and remarks. The morphology of these pharyngeal teeth, such as the lateral compression, and the triangular shape on the top, have similarities to modern Barbini specimens consulted in the comparative collection housed at the University of Tübingen. Due to the lack of comprehensively studied and comparative material on the pharyngeal dentition of extant barbins, we prefer to assign these remains to the tribe Barbini.

Cyprinidae indet.

Fig. 2F

Material. One fragment of caudal vertebra (IPS-PAM207-20); four fragments of palatine (IPS-PAM207-20–IPS-PAM207-24).

Description and remarks. The fragment of a caudal vertebra shows the typical narrow centrum in its middle portion, a smooth surface, and a single, well-defined lamella. Several authors have noted that, among cyprinids, it is not possible to be more precise based solely on vertebrae, and therefore their attribution is restricted to the family level (e.g., Prenda et al. 1997; Russ 2010; Guillaud et al. 2020). Based on our observations of the modern comparative collection, the coralliform shape of the grinding surface of the palatine, when palatine "teeth"

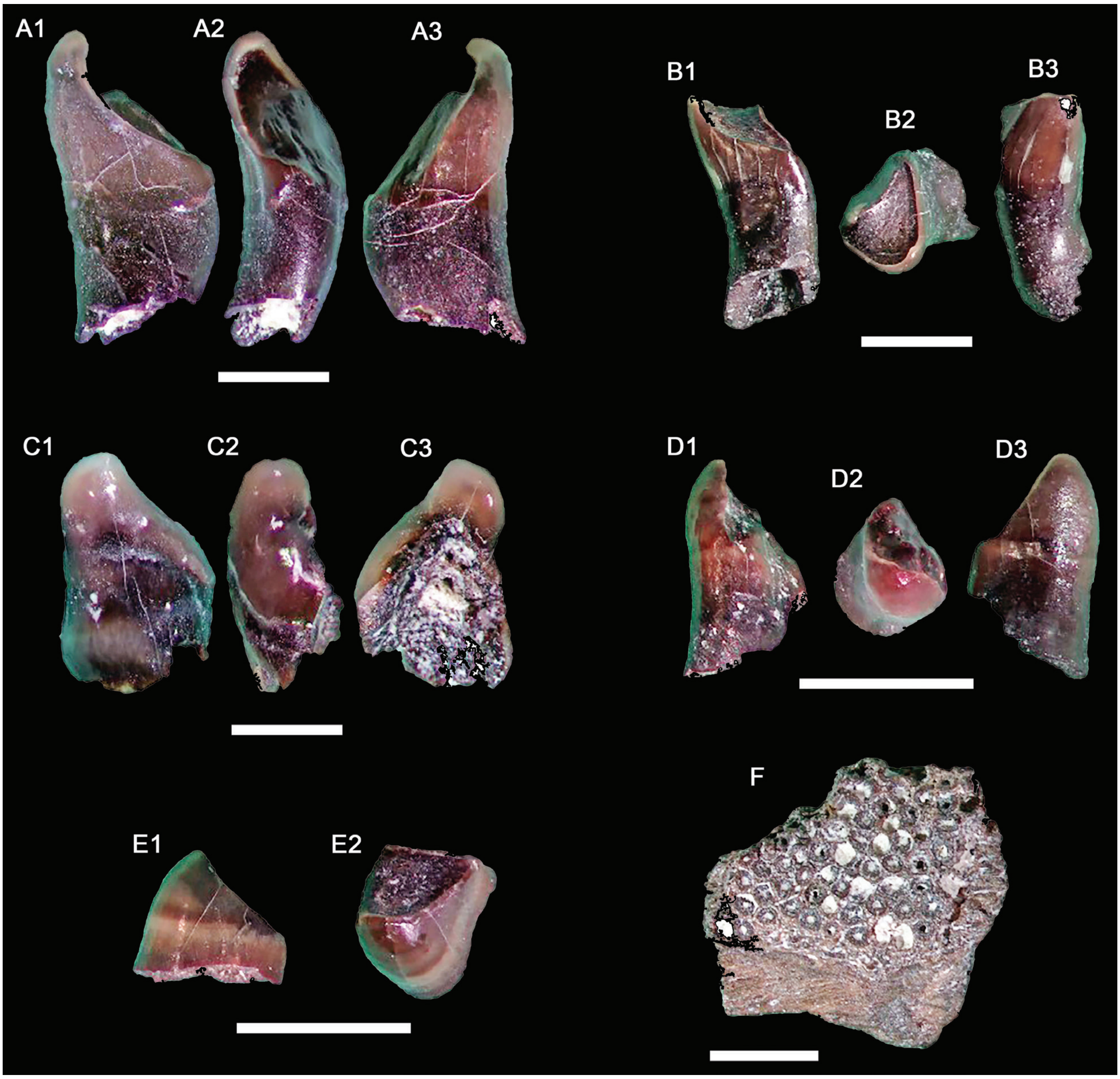

Figure 2. Digital images of fishes from PAM 207 (Late Miocene, Ouarzazate Basin, central-south Morocco). **A, B.** *Luciobarbus* sp.; **A.** Pharyngeal tooth in medial (**A1**), occlusal (**A2**), and lateral (**A3**) views (IPS-PAM207-16); **B.** Pharyngeal tooth in medial (**B1**), occlusal (**B2**), and lateral (**B3**) views (IPS-PAM207-15). **C–E.** Barbini indet.; **C.** Pharyngeal tooth in medial (**C1**), occlusal (**C2**), and lateral (**C3**) views (IPS-PAM207-19); **D.** Pharyngeal tooth in medial (**D1**), occlusal (**D2**), and lateral (**D3**) views tooth (IPS-PAM207-17); **E.** Pharyngeal tooth in medial (**E1**) and occlusal (**E2**) views (IPS-PAM207-18). **F.** Palatine fragment of Cyprinidae indet. in occlusal view (IPS-PAM207-23). Scale bars: 1 mm.

are missing, shows similarities to the palatines of cyprinids, and we tentatively assign these elements to the family Cyprinidae. Due to the fragmentation of the bones, a more detailed attribution is not possible.

Teleostei indet.

Material. Four neural spines (IPS-PAM207-25–IPS-PAM207-28).

Description and remarks. Four incomplete fragments of neural spines were recovered, showing their typical serrated morphology. Any further identification of this material is not possible.

Class Amphibia Gray, 1825
Order Anura Duméril, 1805
Family Alytidae Fitzinger, 1843
Subfamily Discoglossinae Günther, 1858

Gen. et sp. indet.

Fig. 3A–L

Material. Four fragments of maxillae (IPS-PAM207-31–IPS-PAM207-34), one left prearticular (IPS-PAM207-35), 25 vertebrae (IPS-PAM207-36–IPS-PAM207-60), one sacrum (IPS-PAM207-61), two urostyles (IPS-PAM207-62, IPS-PAM207-63), 11 radioulnae (IPS-PAM207-64–IPS-PAM207-74), ten right and six

Figure 3. Digital images of amphibians and reptiles from PAM 207 (Late Miocene, Ouarzazate Basin, central-south Morocco). **A–L.** Discoglossinae indet.; **A.** Maxilla in medial (**A1**) and lateral (**A2**) views (IPS-PAM207-31); **B.** Left prearticular in dorsal (**B1**), medial (**B2**), and lateral (**B3**) views (IPS-PAM207-35); **C.** Vertebra in ventral view (**C1**), anterior (**C2**), and posterior (**C3**) views (IPS-PAM207-37); **D.** Sacrum in dorsal (**D1**), ventral (**D2**), anterior (**D3**), and posterior (**D4**) views (IPS-PAM207-61); **E.** Urostyle in dorsal (**E1**), left lateral (**E2**), and anterior (**E3**) views (IPS-PAM207-62); **F.** Radioulna in medial (**F1**), ventral (**F2**), and lateral (**F3**) views (IPS-PAM207-64). **G–J.** Left (**J**, **H**) and right (**G**, **I**) ilia in lateral (**G, J1, H1, I1**) and medial (**J2, H2, I2**) views (IPS-PAM207-75, IPS-PAM207-78, IPS-PAM207-81); **K.** Femur in lateral view (IPS-PAM207-91); **L.** Tibiofibula in lateral views (IPS-PAM207-95). **M.** *Ophisaurus* sp. parietal in dorsal (**M1**) and ventral (**M2**) views (IPS-PAM207-29). Scale bars: 1 mm.

left ilia (IPS-PAM207-75, IPS-PAM207-90), four femora (IPS-PAM207-91–IPS-PAM207-94), and 21 tibiofibulae (IPS-PAM207-95–IPS-PAM207-115).

Description. Some differences in size are present among the fossil remains, but morphologically they are very homogeneous, suggesting that they may all belong to a single species, represented mainly by juvenile specimens and a few subadults.

Maxillae. These are mainly represented by small fragments that cannot be precisely localized within the element as a whole (Fig. 3A). All bear numerous pedicellate teeth (or at least tooth positions); the horizontal lamina is consistently relatively thick, and the lateral surface lacks dermal ornamentation.

Prearticular. The only prearticular preserved is small, well curved, and relatively complete, documenting the medial part of the element (Fig. 3B). The sulcus for Meckel's cartilage at the level of the process area is shallow. The coronoid (and possibly paracoronoid) process is broken.

Vertebrae. All fossil vertebrae are small (centrum length = 1.28 ± 0.4 mm; min. = 1.0 mm; max. = 3.0 mm; n = 20), and only the centrum and the base of the transverse processes are preserved (Fig. 3C). The vertebrae are opisthocoelous, with an anterior condyle and a posterior cotyle that is rounded or slightly dorsoventrally flattened.

Sacrum. The sacrum is relatively well preserved and includes the neural arch, part of the transverse processes, and part of the centrum (Fig. 3D). In dorsal view, two robust transverse processes are clearly visible and extend slightly anteroposteriorly. The neural crest is thick, moderately high, and hourglass-shaped. In anterior view, the bases of the transverse processes appear moderately robust. In ventral view, the centrum is largely incomplete but clearly shows two posterior condyles that are well separated and somewhat dorsoventrally flattened. The presence of an anterior condyle is less evident but appears probable.

Urostyles. One of the two urostyles is relatively complete (Fig. 3E), while the other preserves only the anteriormost part, lacking the transverse processes and dorsal crest. In anterior view, the two cotylar cavities are circular and well separated by a vertical septum. The insertion of one of the transverse processes is visible on the urostyle with the best preservation. In lateral view, this insertion is relatively wide, and there is a well-developed horizontal lamina present posterior to the transverse process.

Radioulnae. All radioulnae are fragmented and preserve only the proximal part of the element, i.e., the well-ossified capitulum and a more or less extended portion of the strongly constricted collum antibrachii (Fig. 3F).

Ilia. All fossil ilia correspond to the posterior part of the bone and mainly preserve the acetabular cavity and the tuber superior (Fig. 3G–J). The tuber superior is situated in front of the acetabulum and is elongate and somewhat bulbous. The supraacetabular fossa is poorly developed. The pars ascendens, preserved in only one ilium, is rather elongate and in front of the acetabulum (Fig. 3G). A few ilia preserve the dorsal crest (Fig. 3H–J), which is relatively low, with its highest point at the anterior end of the tuber superior. The pars descendens is generally very narrow (and often intercepted by the ventral margin of the acetabulum), and together with the pars cylindriformis forms an obtuse angle (>120–125°), unlike in *Discoglossus*, where this angle is generally less than 120° (Sanchiz and Alcover 1984; Hossini 2000; Blain et al. 2011). In posterior view, the junction surface with the ischium and pubis is thin and shows a relatively wide, deep sulcus interiliacus. The tuber interiliacus appears to be absent or only weakly developed.

Femora. All femora are fragmented (example in Fig. 3K), preserving only the medial part of the diaphysis. They are sigmoid and relatively well curved. None appears to bear a femoral crest.

Tibiofibulae. The tibiofibulae are also incomplete (example in Fig. 3L), preserving mainly the central part of the bone at the level of the foramen nutritium. No extremity is preserved. Overall, they appear to have been quite elongate and gracile, with some degree of medial constriction.

Remarks. Here, we follow the classification proposed by Sanchiz (1998), according to which the subfamily Discoglossinae is an osteologically well-delimited stem-based group that includes the living and fossil *Discoglossus*, as well as the extinct genera *Eodiscoglossus*, *Latonia*, *Latoglossus*, and *Wealdenbatrachus*. Clear attribution to the subfamily Discoglossinae can be made on the basis of a toothed maxilla, a urostyle bearing transverse processes and with two anterior cotyles for articulation with the sacrum, a rather long pars ascendens, and the presence of a low dorsal crest and sulcus interiliacus on the ilium. The fact that the coronoid area is broken in the only preserved prearticular hampers any comparison with other fossil genera, and PAM 207 fossils are thus referred here to Discoglossinae indet.

However, among Discoglossinae, the PAM 207 discoglossines differ from modern *Discoglossus* in the morphology of the ilium, particularly in the angle between the pars descendens and the pars cylindriformis. This angle is more obtuse in our fossils, similar to that observed in the genera *Latonia* and *Latoglossus*. The PAM 207 discoglossines also differ from the '*Discoglossus*' from the Middle Miocene of Beni Mellal (Vergnaud-Grazzini 1966) in that the ilia from PAM 207 have a narrower pars descendens. Although the material is relatively small, it does not morphologically differ from *Latoglossus zraus*, the only named genus and species of the family Alytidae represented in the Middle–Upper Miocene of Morocco (Hossini 2000). In conclusion, the fossils from PAM 207 may be referred either to *Latoglossus zraus* or the unidentified *Latonia*-like small discoglossine frog from Guefait 1 A (Blain el al. 2013).

PAM 207 corresponds to the fourth record of a fossil discoglossine frog in the Miocene of Morocco, following *Latoglossus zraus* from the Upper Miocene (Vallesian) of Oued Zra (Hossini 2000), Alytidae indet. (*Latoglossus*?) from the Middle Miocene of Beni Mellal (Vergnaud-Grazzini 1966; Hossini 2000), and Alytidae indet. from the Late Miocene of Guefaït 1A (Blain et al. 2013).

Class Reptilia Laurenti, 1768
Order Squamata Oppel, 1811
Suborder Anguimorpha Furbringer, 1900
Family Anguidae Gray, 1825
Subfamily Anguinae Gray, 1825
Genus *Ophisaurus* Daudin, 1803

Ophisaurus sp. sensu lato

Fig. 3M

Material. One parietal (IPS-PAM207-29).

Description. ***Parietal.*** The fossil corresponds to the posterior right part of the parietal table (***lamina parietalis***).

The supratemporal processes are broken, but the right one, which preserves its anteriormost portion, appears to have diverged posteriorly. In dorsal view (Fig. 3M1), a well-developed dermal ornamentation is present on the dorsal surface of the parietal table, and the frontoparietal, interparietal, lateral, and occipital shields are clearly recognizable. Laterally, the limits of this ornamented surface appear to contact the lateral margins of the bone, while posteriorly it does not reach the posterior margin of the parietal table due to the presence of a large, smooth area (***area levis***). The ornamentation consists of isolated pits, sometimes located in deep grooves and weak ridges, with a convex posterior limit ending near the arcuate edge. Posteriorly, the arcuate carina is rounded and likely extended on each side along the parotid process. A wide, elliptical pineal foramen is present in the middle of the table. Based on the position of the foramen relative to the posterior margin of the parietal, the fossil does not appear to have been particularly elongated, although this is probably because it represents a juvenile. In ventral view (Fig. 3M2), the ventral crests are visible on the smooth ventral surface. The anterolateral and posterolateral crests contact each other, as do the anterolateral and medial crests. The contact of the anterolateral ventral crest with the medial ventral crest typically splits the margin of the parietal fossa into two sections, referred to as the ***crista juxtafovealis*** (anterior to the contact) and ***crista postfovealis*** (posterior to the contact) following Klembara et al. (2010). However, due to breakage, the postfoveal crest is not visible in this fossil. The parietal fossa appears to be inverted V-shaped, narrow, and deep, and is cut off at mid-length by the arched carina. No parietal notch is visible posteriorly, and the posterior portion of the wide parietal fossa is observable in ventral view.

Remarks. The clade Anguinae currently comprises three extant genera: *Anguis* (Europe and Western Asia), *Ophisaurus* (sensu Klembara et al. 2014; i.e., including *Dopasia* and *Hyalosaurus* from North America, Northern Africa, and Southeast Asia), and *Pseudopus* (southeastern Europe to Central Asia). There is abundant fossil data on this clade in Europe from the Eocene to the Early Pleistocene (see Loréal 2025, for a recent update). However, fossil data from North Africa are much rarer. Anguid lizards (Anguidae indet.) are known from the Middle Miocene of Beni Mellal (Morocco; Rage 1976) and the Late Miocene (Vallesian) of Asif Assermo (Morocco; in Stoetzel 2009). *Ophisaurus* s. l. has been reported from the early Late Miocene (Vallesian) of Oued Zra (Morocco; in Stoetzel 2009). *Ophisaurus* sp. has been reported from the Late Miocene of Guefaït 1A (Blain et al. 2013), and cf. *Ophisaurus* from the Late Pliocene–Early Pleistocene of Guefaït 2 and 4 (unpublished observations) and from the Pleistocene of Irhoud Ocre (Morocco) (in Stoetzel 2009). At least the extant Moroccan species *O. koellikeri* has been documented at the Plio-Pleistocene transition of Ahl al Oughlam (Morocco; Bailon 2000) and in the Holocene layers of El Harhoura 2 (Morocco; Stoetzel et al. 2008). The anguid lizards from the Middle Miocene of Beni Mellal have not been illustrated, but according to Rage (1976) they differ from *Ophisaurus*.

The fragmentary fossil parietal from PAM 207 differs from the genera *Pseudopus* and *Smithosaurus* by the apparent absence of the *facies muscularis* (muscular surface), which is well developed in extant and fossil *Pseudopus* (Klembara 1979) and in the extinct *Smithosaurus* (Early Miocene of Germany; Vasilyan et al. 2022). In addition, the occipital shield is usually much more developed in *Pseudopus* than in the fossil. In *Anguis*, the cranial parietal crest is usually better developed, especially at its junction with the ventrolateral ridge; the anterior end of the ventrolateral ridge of the supratemporal process is located more anteriorly on the bone; and the smooth area (*area levis*) is relatively reduced. According to Klembara (2012), Klembara et al. (2017), and Klembara and Rummel (2018), the *area levis* is shorter than the occipital shield in *Anguis*, whereas it is as long as the shield in *Pseudopus* and *Ophisaurus*. However, Villa and Delfino (2009) suggest a certain degree of variation in this feature. The absence of a parietal notch may be another character distinguishing the fossil from *Anguis* gr. *An. fragilis*; however, according to Villa and Delfino (2019), the development of the parietal notch undergoes ontogenetic variation in this taxon, with its depth increasing during growth.

Attribution to *Ophisaurus* sensu lato relies on the posterior position of the parietal fossa, which is deep and cut at mid-length by the arcuate carina. Comparison among the different species of the genus is hampered by the fragmentary state of the fossil, as well as by the possibility that it represents a juvenile individual.

Class Mammalia Linnaeus, 1758
Order Eulipotyphla Waddel, Okada & Hasegawa, 1999
Family Soricidae Fischer, 1814
Subfamily Crocidosoricinae Reumer, 1987
Tribe Oligosoricini Gureev, 1971
Genus *Lartetium* Ziegler, 1989

Lartetium africanum (Lavocat, 1961)

Fig. 4A, B

Material and measurements. One right i1 (L: 1.90) (IPS-PAM207-30), one left m1 (L: 1.25; TRW: 0.82; TAW: 0.91) (IPS-PAM207-31).

Description. ***i1*** (Fig. 4B). The i1 is a bicuspulate element. The root is almost equal in length to the crown. The crown and the root display only an inconspicuous bending between both, almost standing along a straight axis. There is a well-developed cingulid covering the labial base of the enamel.

m1 (Fig. 4A). The m1 has a talonid wider than the trigonid, although both parts of the tooth are quite similar in length. The protoconid is the highest cuspid of the tooth, followed by the metaconid and the hypoconid. The entoconid is a small cone-shaped cuspid placed just anteriorly from an almost completely reduced entostylid. The paraconid is quite similar in height to the entoconid.

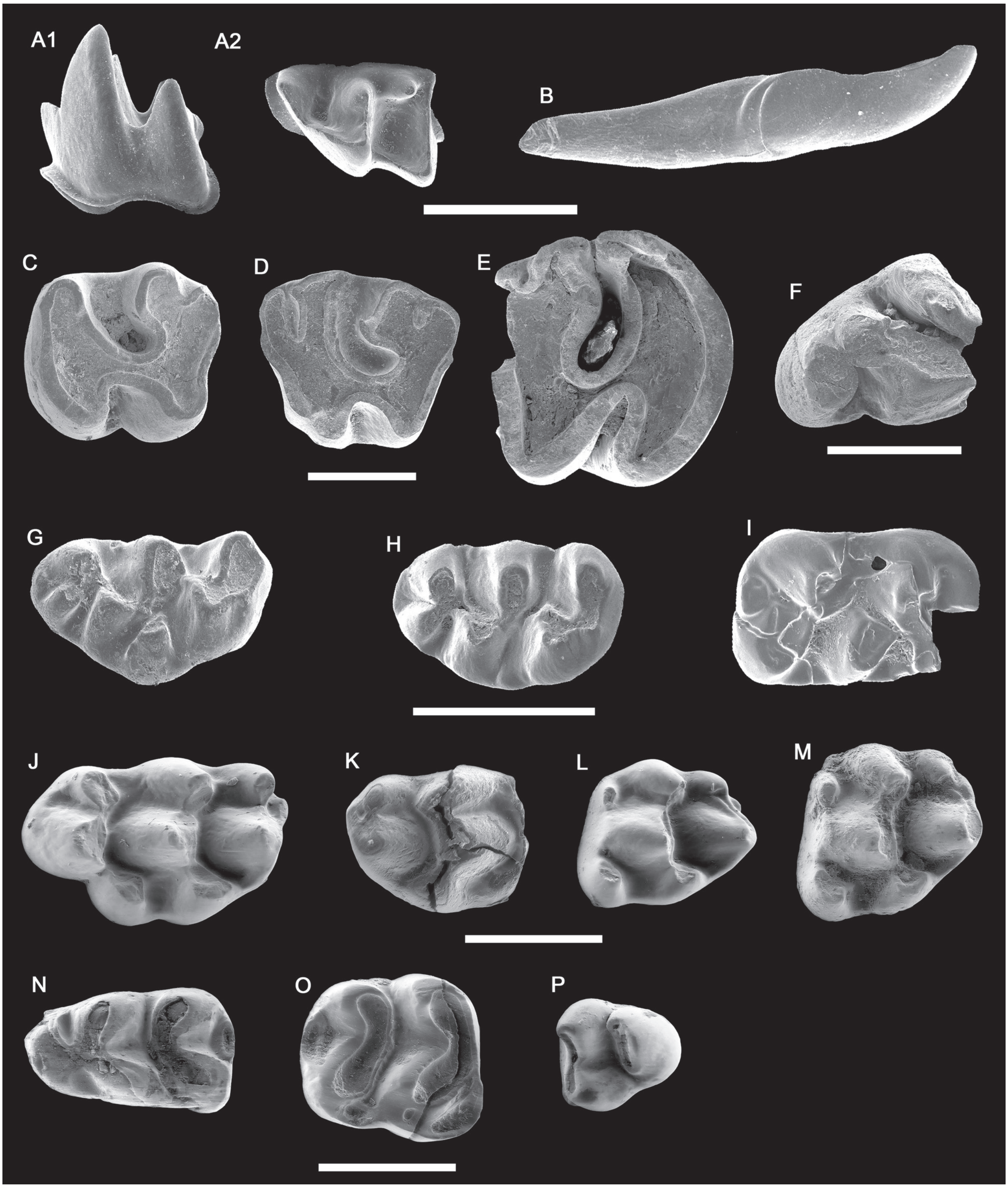

Figure 4. ESEM images of insectivores and rodents from PAM 207 (Late Miocene, Ouarzazate Basin, central-south Morocco). **A, B.** *Lartetium africanum*. **A.** Left m1 in labial (**A1**) and occlusal (**A2**) views (IPS-PAM207-31); **B.** Right i1 in labial view (IPS-PAM207-30). **C–E.** *Africanomys* sp.; **C.** Left DP4 in occlusal view (IPS-PAM207-14); **D.** Left DP4 in occlusal view (IPS-PAM207-09); **E.** Right M1-2 in occlusal view (IPS-PAM207-08); **F.** Right m3 of *Zramys* cf. *salemi* in occlusal view (IPS-PAM207-10). **G–I.** *Myocricetodon* cf. *ouaichi*; **G.** Left M1 in occlusal view (IPS-PAM207-02); **H.** Left M1 in occlusal view (IPS-PAM207-03); **I.** right m1 in occlusal view (IPS-PAM207-13). **J–P.** *Progonomys mauretanicus*; **J.** Left M1 in occlusal view (IPS-PAM207-01); **K.** Fragment of right M1 in occlusal view (IPS-PAM207-04); **L.** Left M2 in occlusal view (IPS-PAM207-06); **M.** Left M2 in occlusal view (IPS-PAM207-05); **N.** Left m1 in occlusal view (IPS-PAM207-12); **O.** Right m2 in occlusal view (IPS-PAM207-11); **P.** Left m3 in occlusal view (IPS-PAM207-00). Scale bars: 1 mm.

The blades of the protolophid and the paralophid are remarkably notched. The hypolophid and the oblique cristid descend regularly from the hypoconid towards the entostylid, and to the middle height of the protoconid, respectively. A marked labial cingulid outlines the base of the paralophid in occlusal view.

Remarks. In the preliminary identification of the material (Tesón et al. 2010), this taxon could only be identified to the tribe level, following the proposal of Furió et al. (2007). Considering the relative lengths of the talonid and trigonid of the m1, and the slight bending between the root and the crown of the lower incisor, this form was classified as an archaic member of the family Crocidosoricinae, more specifically as an undetermined Oligosoricini species.

The study by Hugueney et al. (2015), describing unpublished material of *Lartetium africanum*, shed new light on the oldest fossil shrews from the African continent. Beyond the extreme similarities in the morphologies of i1 and m1, the measurements of these elements from the Ouarzazate material fall entirely within the range of the Beni Mellal assemblage, as provided by Hugueney et al. (2015): (FSL 66873) m1: L=1.26 × TRW=0.83 × TAW=0.93; (FSL 66874) m1: L=1.20 × TRW=0.80 × TAW=0.88; (FSL 66875) m1: L=1.28 × TRW=0.87 × TAW=0.93; and (FSL 66876) i1: L=1.98.

In the absence of any alternative hypothesis that could challenge this ascription, this identification likely indicates a species that persisted in North Africa for several million years without undergoing any remarkable change in size or morphology.

Order Rodentia Bowdich, 1821
Family Ctenodactylidae Zittel, 1893
Genus *Africanomys* Lavocat, 1961

Africanomys sp.

Fig. 4C–E

Material and measurements. One left DP4 (L: 2.24; W: 1.93) (IPS-PAM207-14); one left DP4 (L: 2.09; W: 1.86) (IPS-PAM207-09); one right M1-2 (L: ca. 2.64; W: 2.70) (IPS-PAM207-08).

Description. ***DP4*** (Fig. 4C, D). The available specimens are highly worn. The anteroloph is still present in IPS-PAM207-14 (Fig. 4C), separated from the protoloph by a small anterosinus. In IPS-PAM207-09 (Fig. 4D), the anteroloph, protoloph, and paracone are fused. A deep mesosinus is present, directed backwards. A very shallow anteriorly directed sinus is also present. An obliquus to transverse longitudinal ridge is observable. The metacone and hypocone are widely connected. A small labial posterolophid delimits a very small posterosinus.

M1-2 (Fig. 4E). The dental pattern is very simple, formed by two lobes: an anterior lobe (including the anteroloph, protocone, and paracone) and a posterior lobe (including the metacone, hypocone, and posteroloph). A small posterosinus is present between the hypocone and the posteroloph. Both lobes are connected by an oblique longitudinal ridge. The sinus is short and directed forward. The mesosinus is deep and directed backwards.

Remarks. The teeth of *Africanomys* from PAM 207 correspond to a very large species, largely exceeding the size of *Africanomys pulcher*, *Africanomys minor*, and *Africanomys kettarati* (see Lavocat 1961; Jaeger 1977). They fall within the upper limits of variability of *A. major* from the site of Pataniak 6 (Jaeger 1977; Gunnell et al. 2016). To date, the youngest record of *Africanomys* is from the Vallesian site of Oued Zra, with *A. kettarati* (Jaeger 1977). However, the presence of *Africanomys* sp. at PAM 207 indicates that some representatives of this genus persisted into the early Turolian. *Africanomys* sp. from PAM 207 can be clearly distinguished from the representatives of the genus *Irhoudia* (Jaeger 1977; Mahboubi et al. 2022) by the presence of anterosinus and posterosinus.

Family Gerbillidae Alston, 1876
Subfamily Myocricetodontinae Lavocat, 1961
Genus *Zramys* Jaeger & Michaux, 1973

Zramys cf. *salemi* Jaeger, 1977

Fig. 4F

Material and measurements. One fragment of right M1-2 (IPS-PAM207-07) (W: 1.30); one right m3 (L: ca. 1.99; W: 1.44) (IPS-PAM207-10).

Description. ***m3*** (Fig. 4F). The anterior wall of the tooth is absent, but a very low, residual labial anterolophid can still be recognized at the base of the protoconid. A deep mesosinusid is directed forward. A transverse, deep sinusid is also present. The hypoconid and entoconid are fused, forming a round cusp, with no evidence of a posterosinusid.

Remarks. Although in the preliminary classification by Tesón et al. (2010) the m3 of *Zramys* from PAM 207 was assigned to *Zramys* cf. *hammamai*, this tooth is larger than that species, as well as larger than the m3 of *Zramys gueltae*, *Zramys dubius*, *Zramys semmnensis*, *Zramys jaegeri*, and *Zramys cavatus* (see Jaeger et al. 1973; Jaeger 1977; Robinson et al. 1982; Ameur 1984; Coiffait-Martin 1991). In size, it matches the m3 of *Zramys haichai* from Oued Zra (Morocco) and *Zramys salemi* from the type locality of Sidi Salem (Algeria; Jaeger et al. 1973). However, the m3 from PAM 207 exhibits a more simplified pattern than the m3 of *Z. haichai* from Oued Zra, with the hypoconid-entoconid pair reduced to a single round cusp, not delimiting a ring as in the type population of Oued Zra (Jaeger 1977, pl. 4, fig. 7). Therefore, we refer this material to *Zramys* cf. *salemi*. In addition to the m3, a fragment of M1-2 retains the labial wall of the paracone and the hypocone. The posterior ectoloph of the paracone does not reach the anterior wall of the hypocone.

Genus *Myocricetodon* Lavocat, 1961

Myocricetodon cf. *ouaichi* Jaeger, 1977

Fig. 4G–I

Material and measurements. One left M1 (L: 1.66; W: 0.93) (IPS-PAM207-02); one left M1 (L: 1.57; W:

0.95) (IPS-PAM207-03); one right m1 (L: 1.55; W: 1.00) (IPS-PAM207-13).

Description. ***M1*** (Fig. 4G, H). A low cingulum is present on the anterior wall of both teeth. The anterocone is composed of two alternating lobes, separated by a groove. The anterior arm of the protocone is connected to the labial lobe of the anterocone. The posterior wall of the protocone is connected to the lingual wall of the paracone. A well-developed, isolated lingual accessory cuspule is present in one of the teeth (Fig. 4G) but absent in the other (Fig. 4H). The anterior arm of the hypocone is connected directly to the posterior wall of the paracone in one case (IPS-PAM207-02), while in the other tooth the hypocone and paracone are isolated (IPS-PAM207-03). The hypocone is connected posteriorly to the metacone.

m1 (Fig. 4I). Although broken, it appears that the anteroconid was wide. A well-developed lingual anterolophid is present. The protoconid is directly connected to the metaconid. There is no longitudinal ridge, the sinusid being connected to the mesosinusid, separating the protoconid from the entoconid. The hypoconid and entoconid are directly connected. A small, rounded posterolophid is present.

Remarks. The sample of *Myocricetodon* from PAM 207 was preliminarily assigned to *Myocricetodon* cf. *afoudensis*. New comparisons reveal that the studied sample shows larger dimensions than those of this species (Benammi 2001). Similarly, the studied teeth are larger than those of *Myocricetodon jaegeri* (see Benammi 2001). In contrast, the M1 fits both in size and morphology with *Myocricetodon seboui* from Oued Zra and Guefait-1 (Jaeger 1977; Agustí et al. 2023), and *Myocricetodon ouaichi* from Tafna 2 (Mahboubi et al. 2015). The dimensions of the m1 fall within the upper limit of variability of *M. seboui* and match the size of *M. ouaichi*. Although fragmented, the anteroconid of the m1 exhibits a more complex morphology than the small, simple, rounded anteroconid of *M. seboui*. In contrast, it matches the wider anteroconid of *M. ouaichi*, described for the first time by Coiffait-Martin (1991), which has a large anteroconid and a well-developed labial anterolophid.

Family Muridae Illiger, 1811
Subfamily Murinae Illiger, 1811
Genus *Progonomys* Schaub, 1938

Progonomys mauretanicus Coiffait-Martin, 1991

Fig. 4J–P

Material and measurements. one left M1 (L: 2.05; W: 1.27) (IPS-PAM207-01); one fragment of right M1 (W: 1.16) (IPS-PAM207-04); one left M2 (L: 1.49; W: 1.32) (IPS-PAM207-05); one left M2 (L: 1.39; W: 1.17) (IPS-PAM207-06); one left m1 poorly preserved (IPS-PAM207-12); one right m2 (L: 1.44; W: 1.25) (IPS-PAM207-11); one left m3 (L: 0.98; W: 0.88) (IPS-PAM207-00).

Description. ***M1.*** (Fig. 4J, K) The t1 is displaced posteriorly relative to the t3. The t1bis and the t2bis are absent. A short spur on the t3 is directed toward the t5–t6 intersection. There is no connection between the t5 and the t1 or t3. A spur on the t6 is directed toward the t9, but both tubercles are widely separated. The t4 and t8 are basally connected by a low, thin ridge. The t7 is absent. The low, well-developed t12 is connected to the t8 but remains separated from the t9.

M2. (Fig. 4L, M) The t1 and t3 are isolated and oval, the former being larger than the latter. The t4 is connected basally to the t8 by a low, narrow ridge. A deep valley separates the t6 and t9. The t7 is absent. There is a small, low t12 attached to the intersection between the t8 and t9.

m1. (Fig. 4N) The only m1 is poorly preserved anteriorly and labially. However, it can be distinguished that the labial cingulum reaches the anteroconid. The anteroconid complex is connected to the metaconid–protoconid complex. The protoconid and hypoconid are slightly displaced posteriorly relative to the metaconid and entoconid. The longitudinal spur is absent. The oval-compressed posterior cingulum is slightly displaced lingually.

m2. (Fig. 4O) The only specimen is somewhat worn. There is no longitudinal spur. The labial cingulum is moderately developed and bears a large labial anteroconid. The small posterior accessory cuspid (c1) is attached to the hypoconid. Another small, rounded accessory labial cuspid is attached to the protoconid. The posterior cingulum is oval.

m3. (Fig. 4P) The hypoconid-entoconid pair (posterior complex) is separated from the protoconid-metaconid complex. Neither the labial anteroconid, labial cingulum, nor posterior accessory cuspid (c1) is present.

Remarks. Originally, the murid sample from PAM 207 was identified as *Paraethomys* cf. *miocaenicus* (see Tesón et al. 2010). However, the separation between the t6 and t9 in the M1 and M2 allows us to discard its assignment to this genus. By contrast, the examined teeth show features characteristic of the genus *Progonomys*, including their small size, elongated and narrow shape, the posterior placement of the t1 relative to the t3, the connection between the t4 and t8, the clear separation of the t6 and t9, the absence of t7, and an overall lack of longitudinal connections.

The PAM 207 sample can be distinguished from *Progonomys minus* (Turkey; Sen, 2003), *Progonomys morganae* (Siwalik; Pakistan; Kimura et al. 2017), *Progonomys shalaensis* (China; Qiu and Li 2016), and *Progonomys manolo* (Lebanon; López-Antoñanzas et al. 2019) by its larger size. *Progonomys hispanicus* (Spain; Michaux 1971), *Progonomys debruijni* (Pakistan; Jacobs 1978), and *Progonomys yunnanensis* (China; Qiu and Storch 1990) were excluded from the genus *Progonomys* by Mein et al. (1993). Nevertheless, the studied teeth are larger than those of these three species. By comparison, *Progonomys woelferi* (Europe; Bachmayer and Wilson 1970) and *Progonomys sinensis* (China; Qiu et al. 2004) are distinguished from the studied molars by their larger size.

In North Africa, two species of *Progonomys* have been recorded: *Progonomys cathalai* and *Progonomys mauretanicus*. The specimens from PAM 207 fall within the uppermost part of the size range of *Progonomys cathalai* from its type locality (Montredon, France; Michaux 1971), with the exception of the m2, which is distinctly larger than those from Montredon. Similarly, the teeth from PAM 207 reach the upper size limit of *Progonomys cathalai* from Masía del Barbo 2B (Spain; Van de Weerd 1976), Híjar (Spain; Brandy 1979), and Montredon niveau supérieur (France; Aguilar 1982). However, the sample from PAM 207 exceeds the size of *Progonomys cathalai* from Guefaït-1 (Morocco; Agustí et al. 2023), Peralejos A (Spain; Van de Weerd 1976), La Bastida (Spain; Agustí 1981), Bayraktepe II (Turkey; Ünay 1981), and Biodrak (Greece; de Bruijn 1976), among others. Furthermore, the studied specimens display more derived traits than *Progonomys cathalai*, such as the presence of a slight ridge on the t6 of M1. For these reasons, attribution to *Progonomys cathalai* can be confidently ruled out.

The molars of *Progonomys* from PAM 207 exhibit diagnostic traits of *Progonomys mauretanicus*, including the absence of a connection between t1 and t5, the presence of a spur on t3 and a very slight crest on t6 in M1, the absence of a connection between t6 and t9 in M2, and a labial cingulum reaching the anteroconid in m1. Moreover, the size range of the studied molars corresponds to that of *Progonomys mauretanicus* from its type locality (El Hiout), and Mekhencha, Maatgua, Oued el Arbi, and Bab el Ahmar (Algeria; Coiffait-Martin 1991), except for the M1 fragment (IPS-PAM207-04) and the m3 (IPS-PAM207-00), which are slightly smaller. By comparison, the samples of *Progonomys mauretanicus* from Guergour Ferroudj and Zighout Youcef (Jaeger 1977; Coiffait-Martin 1991)are slightly larger than those from PAM 207. Considering both morphological and biometric criteria, the specimens from PAM 207 are identified as *Progonomys mauretanicus*.

The earliest evidence of *Progonomys* in North Africa dates back to at least 11 Ma, as indicated by the record of *Progonomys cathalai* in Bou Hanifia 5 (10.9 Ma; Sen 1986). This suggests that the genus may have dispersed simultaneously towards both the northern and southern Mediterranean margins (Jaeger et al. 1977; Coiffait-Martin 1991; Agustí et al. 2023). The arrival of *Progonomys* in North Africa from southern Asia likely occurred via the Levant corridor, while its entry into Europe is thought to have followed an eastern Asian route (López-Antoñanzas et al. 2019). *Progonomys mauretanicus* is considered a phyletic descendant of *Progonomys cathalai* in North Africa (Coiffait-Martin 1991). The species has been recorded from several early and middle Turolian (upper Tortonian–lower Messinian) localities in Algeria, including El Hiout, Bab el Ahmar, Bou Adjeb, Guergour Ferroudj, Maatgua, Ouled el Arbi, Sidi Salem, Zighout Youcef, Sidi Messaoud, and Mekhencha, as well as from the site of As Sahabi in Libya (Jaeger 1977; Coiffait-Martin 1991; Agustí 2008; Stoetzel 2013).

Biochronological framework

Rodents are considered excellent tools for making biostratigraphic and biochronological correlations because of their high evolutionary rates, cosmopolitanism, and rapid diversification. The rodent assemblage from PAM 207 indicates that the site is slightly younger than the late Vallesian site of Guefaït 1 (Morocco; Agustí et al. 2023), a locality that shares the presence of *Zramys salemi* but contains *Progonomys cathalai*, the ancestor of *Progonomys mauretanicus*. Biostratigraphically, PAM 207 is very close to Sidi Salem (Jaeger 1977; Coiffait-Martin 1991), where both *Progonomys mauretanicus* and *Zramys salemi* also occur. The early Turolian sites of Bab el Ahmar, Zighout Youcef, Mekhencha, El Hiout, Maatgua, Oued el Arbi, and Sidi Messaoud also record *Progonomys mauretanicus* (Coiffait-Martin 1991). However, they contain *Zramys cavatus*, a species still absent in PAM 207 and Sidi Salem, which instead record *Zramys salemi* together with the late Vallesian Guefait 1. This indicates that PAM 207 and Sidi Salem are slightly older than the other sites. Thus, both PAM 207 and Sidi Salem mark the onset of the early Turolian in North Africa.

PAM 207 yielded a reversed polarity, which was preliminarily correlated with chron C4r (8.77–8.12 Ma) by Tesón et al. (2010). The new rodent identifications from PAM 207, together with comparisons to sites with paleomagnetic or radiometric datings, allow a reevaluation of this correlation. In terms of chronology, Afoud 6 (10.1 Ma; Benammi et al. 1996), Oued Zra (9.7 Ma; Jaeger 1977), and Oued Tabia (9.7 Ma; Benammi 1997) are older than PAM 207, based on the occurrence of *Progonomys cathalai* and *Zramys haichai*. Tafna 2 shares with PAM 207 the occurrence of *Myocricetodon ouaichi*. However, its rodent association also includes *Progonomys cathalai*, indicating an older age than PAM 207. Tafna 2 was correlated with chron C4An (9.10–8.77 Ma; Ogg 2020) by Mahboubi et al. (2015). Therefore, the correlation of the reversed polarity of PAM 207 with C4Ar (9.78–9.10 Ma; Ogg, 2020) can be confidently discarded. Conversely, the presence of *Paraethomys*, *Zramys hamamai*, and *Protatera algeriensis* in Amama 2, dated to 7.7 Ma (Coiffait-Martin 1991), clearly indicates a younger age than PAM 207. Thus, the reversed C4n.1r (8.12–7.70 Ma; Ogg 2020) can also be discarded. Based on this evidence, the previous correlation of the reversed polarity interval with chron C4r (8.77–8.12 Ma) is confirmed.

This chronology is also consistent with the amphibian and reptile record, as the poorly diversified herpetofaunal assemblage from PAM 207, as was already the case for Guefait 1 (Blain et al. 2013), shows the absence of typically tropical African taxa (*Xenopus*, *Ptychadena*, and *Sclerophrys regularis*) that are present in the Middle Miocene of Beni Mellal and the early Late Miocene of Oued Zra, as well as the absence of European taxa that currently form part of the North African herpetofauna and are thought to have entered the Maghreb at the end of the Late Miocene with the closure of the Betic and Rifian Corridors. In contrast, it includes taxa of Eurasian origin (Discoglossinae and *Ophisaurus*), which may have entered North Africa during or prior to the Middle Miocene via the land connection between the Afro-Arabian plateau and Asia established during the Early Miocene.

Considering the various North African Late Miocene sites with radiometric or paleomagnetic datings, some biozones proposed by Stoetzel (2013) can be tentatively constrained. The Vallesian Biozone 3a contains *Progonomys cathalai*, *Zramys dubius/jaegeri*, and *Schizogalerix moedlingensis*, including localities such as Bou Hanifia 1 and Bou Hanifia 2. On the other hand, the Biozone 3b is defined by the presence of *Progonomys cathalai*, *Senoussimys hanifiae*, *Myocricetodon seboui/trerki/ouedi*, *Zramys semmenensis/gueltae/haichai*, *Microdyromys/Afrodyromys chaabi*, *Africanomys kettarati*, and *Irhoudia*, covering localities such as Oued Tabia, Bou Hanifia 5, Asif Assermo, Afoud 6, Oued Zra, Koudiet el Tine, Amama 1, Tafna 2, and Guefaït 1 (Stoetzel 2013, and references therein). The boundary between the two biozones falls between Bou Hanifia 2 and Bou Hanifia 5. Since Bou Hanifia 5 has been dated to 10.9 Ma (Sen 1986; Mahboubi et al. 2015), the lower limit of the Biozone 3b can be assigned to roughly 11 Ma (see Fig. 5). The Biozone 3c marks the beginning of the early Turolian in North Africa and is characterized by the presence of *Progonomys mauretanicus*, *Dendromus* sp., *Zramys salemi*, and *Zramys rhummelensis/cavatus*. This biozone includes the localities of PAM 207, Sidi Salem, Dra Temedlet, Bab el Ahmar, and Zighout Youcef. The boundary between the Biozone 3b and 3c falls between the deposits of Guefait 1 and PAM 207. Based on the correlation of PAM 207 with chron C4r, it can be assigned to approximately 8.7 Ma (Fig. 5). Finally, the Biozone 4a is marked by the presence of *Myocricetodon seboui/asphodelae*, *Zramys cavatus*, and *Protatera algeriensis*, including localities such as Mekhencha, El Hiout, Maatgua, Oued el Arbi, and Sidi Messaoud (Stoetzel 2013, and references therein). In contrast, the Biozone 4b, which represents the onset of the middle Turolian in North Africa, is characterized by the occurrence of *Paraethomys miocaenicus*, *Progonomys mauretanicus*, *Protatera algeriensis*, *Zramys hamamai*, and *Eulmus miocaenicus*. It encompasses localities such as Amama 2, Beni Brahim, and Bou Adjeb. Based on the dating of Amama 2, which records the first occurrence of *Paraethomys* in North Africa (see Coiffait-Martin 1991), the lower limit of the Biozone 4b can be assigned to approximately 7.7 Ma (Fig. 5).

Paleoenvironmental reconstruction

Small vertebrates have been widely used as palaeoclimatic and palaeoecological indicators. Amphibian and reptile species are particularly useful for palaeoenvironmental reconstructions (Blain et al. 2009, 2016b; among others). Fish and rodent assemblages also provide valuable information on the past environmental conditions (e.g. Martín-Suárez et al. 2001; Montuire et al. 2006; Piñero et al. 2016, 2024a, 2024b; Blanco-Lapaz et al. 2021). We provide here a preliminary qualitative palaeoenvironmental inference based on the ecological requirements of the small vertebrate taxa identified at PAM 207.

All identifiable fish material recovered from PAM 207 belongs to the family Cyprinidae. Cyprinids are typically associated with temperate waters (ranging between 10–25 °C). Species of this family occur in a wide variety of environments and display remarkable dietary diversity, including the consumption of arthropods and other fish (e.g., Doadrio 2011; Tissot and Souchon 2010). The only fish remains identified to genus level belong to *Luciobarbus* sp. A common ecological feature of barbels (*Luciobarbus* sp.) is their preference for slow-flowing freshwater sources such as rivers and lakes. In Morocco, this genus is the most common and widely distributed fish taxon. Barbels show broad ecological plasticity, occurring in virtually all aquatic habitats inhabited by fish, including saline systems in desert biotopes (Clavero et al. 2017). In conclusion, the fish remains (*Luciobarbus* sp., Barbininae indet. and Cyprinidae indet.) from PAM 207 provide, for the first time, a more detailed characterization of freshwater ecosystems in Morocco during the Late Miocene, particularly evidencing temperate, slow-flowing freshwater habitats such as rivers, lakes, or swampy environments.

Concerning amphibians and reptiles, the assemblage from PAM 207 includes both terrestrial (*Ophisaurus*) and aquatic (Discoglossinae) taxa, suggesting that animals dying in or near water were more likely to be preserved in the sediments of the locality. In its composition, the PAM 207 assemblage is quite typical of an open-air site, with a higher representation of anurans compared to squamates. Discoglossinae are usually interpreted as taxa living in or near permanent water bodies (sometimes even slightly brackish), such as brooklets, seasonal ponds, and swamps. In North Africa, this group remains very abundant today, especially in the subhumid and humid northern regions, although its distribution extends to pre-Saharan oases (Bons and Geniez 1996; Schleich et al. 1996). The more terrestrial *Ophisaurus* (represented today in North Africa by a single species, *Hyalosaurus koellikeri*) suggests a certain degree of vegetative cover (de Pous et al. 2011; Escoriza and Comas 2015). *Hyalosaurus koellikeri* inhabits forests and woodlands dominated mainly by evergreen oaks (*Quercus ilex* and *Q. suber*).

Regarding the rodent assemblage, *Zramys* cf. *salemi* and *Myocricetodon* cf. *ouaichi* belong to the subfamily Myocricetodontinae, whose extant representatives, *Calomyscus* and *Mystromys*, inhabit Central Asia and South Africa, respectively, in open herbaceous or even arid areas with little to no vegetation. The family Ctenodactylidae (gundis) is represented at PAM 207 by *Africanomys* sp. Gundis are known from the Early Miocene to the present, and today the group comprises five extant species. Living gundis inhabit rocky environments, taking shelter in fissures within desert and semi-desert areas across northern Africa (López-Antoñanzas and Knoll 2011; Cassola 2022; among others). The ecological preferences of *Progonomys* remain uncertain.

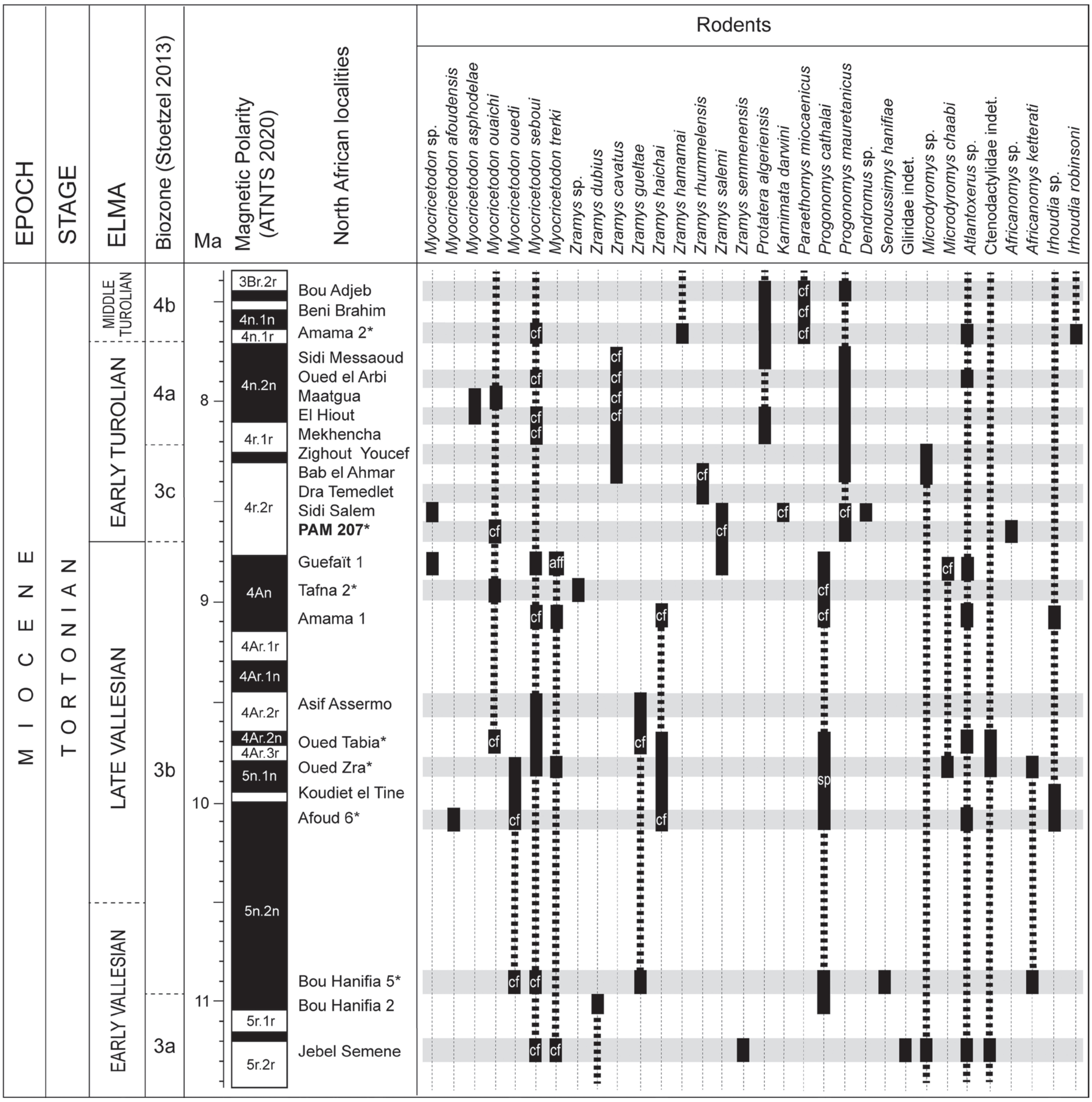

Figure 5. Magnetostratigraphic correlation of PAM 207 and comparison with other northern African localities. The figure also shows the stratigraphic framework of rodents recorded at Late Miocene localities in North Africa. Black squares = presence at the site; dashed line = probable continuity of occurrence even if not recorded. Localities marked with an asterisk are calibrated by palaeomagnetic data: Bou Hanifia 5 (10.9 Ma; Sen 1986; Mahboubi et al. 2015), Afoud 6 (10.1 Ma; Benammi et al. 1996), Oued Tabia (9.7 Ma; Benammi 1997), Tafna 2 (9.1–8.7 Ma; Mahboubi et al. 2015), PAM 207 (Tesón et al. 2010; this work); or by radiometric dating: Oued Zra (9.7 ± 0.5 Ma; Jaeger 1977; 10.1 ± 0.7 Ma; Harland et al. 1982), Amama 2 (7.7 Ma; Coiffait-Martin 1991). Abbreviations: ATNTS, Astronomically Tuned Neogene Time Scale (Ogg 2020); ELMA, European Land Mammal Ages.

Thus, based on comparisons with the ecological requirements of closely related extant rodent species, we infer that during the formation of PAM 207 the landscape was predominantly open and rather arid.

Overall, the ecological affinities of the identified small vertebrates indicate a landscape dominated by open areas with a certain degree of vegetative cover, developed under relatively arid conditions. These environments were associated with temperate freshwater settings in the Ouarzazate Basin around 8.5 Ma, at the beginning of the early Turolian.

Conclusions

The revised small vertebrate assemblage from PAM 207 includes the cyprinid fish *Luciobarbus* sp., the alytid frog Discoglossinae indet., the anguid *Ophisaurus* sp. sensu lato, the soricid *Lartetium africanum*, the ctenodactylid *Africanomys* sp., the gerbillids *Zramys* cf. *salemi* and *Myocricetodon* cf. *ouaichi*, and the murid *Progonomys mauretanicus*.

The rodent assemblage shows that PAM 207 is slightly younger than the Moroccan Guefaït 1 and nearly contemporaneous with the Algerian Sidi Salem, thus representing one of the oldest early Turolian sites in North Africa. Moreover, this comparison places PAM 207 in an intermediate biostratigraphic position between Tafna 2 (9.1–8.7 Ma) and Amama 2 (7.7 Ma), supporting the correlation of the reversed polarity previously observed at PAM 207 with chron C4r (8.77–8.12 Ma).

Based on the new rodent identifications from PAM 207 and comparisons with dated North African sites, the biochronological framework of the region can be refined. Accordingly, the Biozone 3b, proposed by Stoetzel (2013), has a lower limit of roughly 11 Ma, while the boundary between the Biozone 3b and 3c, marking the onset of the early Turolian, is placed at approximately 8.7 Ma. The Biozone 4b, corresponding to the onset of the middle Turolian, has a lower limit assigned to ca. 7.7 Ma. These constraints contribute to the establishment of a chronologically well-defined Late Miocene biochronological framework for North Africa.

Regarding the paleoenvironment, the presence of the fish *Luciobarbus* sp. suggests temperate, slow-flowing freshwater habitats such as rivers, lakes, or swampy environments. The anuran subfamily Discoglossinae is typically interpreted as inhabiting areas in or near permanent water bodies, including brooklets, seasonal ponds, and swamps, even those that are slightly brackish. The occurrence of the lizard *Ophisaurus* sp. points to the existence of a certain degree of vegetative cover. In addition, the rodent assemblage from PAM 207 includes taxa usually associated with arid conditions and open landscapes, such as gerbils and gundis. Altogether, the paleoenvironmental evidence indicates that during the formation of PAM 207, the surroundings of the site were characterized by temperate, slow-flowing freshwater habitats within an open landscape with some vegetative cover. These conditions developed under relatively arid climate at the beginning of the early Turolian in the Ouarzazate Basin.

Competing interests

The authors declare that they have no conflict of interest.

Authors' contributions

The study is based on fieldwork by JA, MF, ET, and AT. ET and AT contributed to the section of geology. The systematic study of fishes was carried out by ABL; the study of herpetofauna by HAB; the study of insectivores by MF; and the study of rodents by JA and PP. Biochronological interpretation was developed by PP, whereas paleoecological interpretations are based on discussions between HAB, PP, and ABL. JA has been responsible for funding acquisition. The manuscript was prepared by PP and managed by MF with contributions from all co-authors.

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