

3D models related to the publication: A new primate community from the earliest Oligocene of the Atlantic margin of Northwest Africa: Systematic, paleobiogeographic and paleoenvironmental implications

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Abstract

This contribution contains the three-dimensional digital models of the dental fossil material of anthropoid and strepsirrhine primates, discovered in Lower Oligocene detrital deposits outcropping in the Porto Rico and El Argoub areas, east of the Dakhla peninsula region (Atlantic Sahara; in the south of Morocco, near the northern border of Mauritania). These fossils were described, figured and discussed in the following publication: Marivaux et al. (2024), A new primate community from the earliest Oligocene of the Atlantic margin of Northwest Africa: Systematic, paleobiogeographic and paleoenvironmental implications. *Journal of Human Evolution*. <https://doi.org/10.1016/j.jhevol.2024.103548>

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INTRODUCTION

We present here the three-dimensional (3D) digital models of a set of dental fossil specimens of primates (Fig. 1; Table 1) that were unearthed in detrital estuarine sediments dating from the earliest Oligocene (Benammi et al., 2019). These sediments are exposed in the westernmost part of North Africa (Atlantic Sahara), on the continental shore of the *Rio de Oro*, east of the Dakhla peninsula (in the south of Morocco, near the northern border of Mauritania). The fossil-bearing localities situated in the sectors of Porto Rico (Pto) and El Argoub (Arg), correspond to the uppermost part of the stratigraphical sequence (Samlat Formation), referred to as Unit 4 (Benammi et al., 2019). Our geological and paleontological surveys since 2013 at the base of that lithological unit of the Pto and Arg sections have allowed for the discovery of a level (Dakhla C2 [DAK C2]) that yielded similar fossil assemblages of marine and estuarine invertebrates and vertebrates, including mammals (see Marivaux et al., 2017a,b, 2019; Benammi et al., 2019). We excavated and collected a total of about five tons of sediment of this level (*ca.* 2500 kg in each spot) over five successive field seasons (2013–2023). Sediments were processed by wet-screening operations. The fossil material consists primarily of bone fragments and isolated teeth, among which the dental specimens of primates reported here (Marivaux et al., 2024). Twenty-two isolated teeth in various stages of preservation (including moderately to very worn/corroded/abraded or broken specimens, as well as pristine ones; Fig. 1) testify to the presence of at least eight primate

species, documenting distinct families, four of which are among the Anthroidea (Oligopithecidae [*Catopithecus* aff. *browni*; Fig. 1A–G], Propliopithecidae [*?Propliopithecus* sp.; Fig. 1H], Parapithecidae [*Abuqatrania* cf. *basiodontos*; Fig. 1I–O], and Afrotarsiidae [*Afrotarsius* sp.; Fig. 1P–Q]) and four among the Strepsirrhini (Djebelemuridae [cf. '*Anchomomys*' *milleri*; Fig. 1S], Galagidae [*Wadilemur* cf. *elegans*; Fig. 1T–U], a possible loriform [*Orogalago saintexuperyi*; Fig. 1V], and an indeterminate strepsirrhine [*Orolemur mermozi*; Fig. 1R]). This record of various primates from the earliest Oligocene of Dakhla represents the first Oligocene primate community from northwest Africa, especially from the Atlantic margin of that landmass (Marivaux et al., 2024). The temporal proximity and faunal resemblance (primate and hystricognath assemblages) between DAK C2 in the west and L-41 in the east (latest Eocene, Fayum; Egypt; e.g., Seiffert, 2012), reveal a widespread east-west distribution of several mammals, thereby underscoring to some extent similar tropical environmental conditions in northern latitudes of Africa during the latest Eocene-earliest Oligocene time interval. The mammal assemblage from the earliest Oligocene of Dakhla shows that primates and rodents (hystricognaths and anomaluroids; Marivaux et al., 2017a,b) were particularly diversified near the drastic global climate change characterizing the Eocene-Oligocene transition (EOT; e.g., Zachos et al., 2008; Bohaty et al., 2012; Westerhold et al., 2020). The mammal record from DAK-C2 occurring within this time window of climatic deterioration, suggests that this tropical region of north-

Inv nr.	Taxon	Description
DAK-Arg-087	<i>Catopithecus</i> aff. <i>browni</i>	Isolated right lower m3 (worn)
DAK-Arg-088	<i>Catopithecus</i> aff. <i>browni</i>	Isolated right lower m2 (abraded/corroded)
DAK-Arg-089	<i>Catopithecus</i> aff. <i>browni</i>	Isolated left lower m1 (worn)
DAK-Pto-052	<i>Catopithecus</i> aff. <i>browni</i>	Isolated right lower m1 (pristine but lacking the mesiobuccal region)
DAK-Arg-090	<i>Catopithecus</i> aff. <i>browni</i>	Isolated left upper P4
DAK-Arg-091	<i>Catopithecus</i> aff. <i>browni</i>	Isolated left upper M2 (worn and corroded)
DAK-Pto-053	<i>Catopithecus</i> aff. <i>browni</i>	Isolated right upper M1 (lacking the buccal region)
DAK-Pto-056	? <i>Propliopithecus</i> sp.	Isolated right lower m3 (fragment of talonid of a germ)
DAK-Arg-092	<i>Abuqatrania</i> cf. <i>basiodontos</i>	Isolated left lower c1
DAK-Arg-093	<i>Abuqatrania</i> cf. <i>basiodontos</i>	Isolated right lower m1
DAK-Arg-094	<i>Abuqatrania</i> cf. <i>basiodontos</i>	Isolated left upper M1 or M2 (corroded, lacking the enamel cap)
DAK-Arg-101	<i>Abuqatrania</i> cf. <i>basiodontos</i>	Isolated left upper M3 (abraded)
DAK-Arg-095	<i>Abuqatrania</i> cf. <i>basiodontos</i>	Isolated right lower i1 or i2
DAK-Arg-096	<i>Abuqatrania</i> cf. <i>basiodontos</i>	Isolated right lower p2 (worn apex)
DAK-Arg-097	<i>Abuqatrania</i> cf. <i>basiodontos</i>	Isolated right lower p2 (worn apex and broken root)
DAK-Arg-098	<i>Afrotarsius</i> sp.	Isolated left lower p3
DAK-Pto-054	<i>Afrotarsius</i> sp.	Isolated right lower m1 (abraded/corroded)
DAK-Arg-099	<i>Wadilemur</i> cf. <i>elegans</i>	Isolated right lower m2
DAK-Arg-103	<i>Wadilemur</i> cf. <i>elegans</i>	Isolated right upper M1 or M2 (lacking the mesial and buccal regions)
DAK-Arg-100	cf. ' <i>Anchomomys</i> ' <i>milleri</i>	Isolated right lower c1
DAK-Arg-102	<i>Orogalago saintexuperyi</i>	Isolated left lower m2 (Holotype)
DAK-Pto-055	<i>Orolemur mermozi</i>	Isolated right upper M1 or M2 (pristine, Holotype)

Table 1. List of models. Collection : PALEVOPRIM (Paléontologie Évolution Paléoécosystèmes Paléoprimatologie) – Université de Poitiers, France.

west Africa was seemingly less affected, if at all, by the cooling and associated paleoenvironmental changes recorded at that time, or at least that the effects were delayed. The fossil specimens are currently housed in the collections of the *Laboratoire Paléontologie Évolution Paléoécosystèmes Paléoprimatologie* (PALEVOPRIM, UMR-CNRS 7262), *Université de Poitiers*, France.

METHODS

The dental specimens figured here were scanned with a resolution of 6 µm, using a µCT-scanning station EasyTom 150/Rx Solutions (Montpellier Ressources Imagerie [MRI], ISE-M, Montpellier, France). AVIZO 2020.2 (Thermo Fisher Scientific) software was used for visualization, segmentation and three-dimensional renderings. These fossil specimens were prepared within a “labelfield” module of AVIZO, using the segmentation threshold selection tool. The crown and roots of each dental specimen were virtually delimited by manual segmentation. The 3D models are provided in “.ply” format, and thus can be opened with a wide range of software programs (e.g., MorphoDig 1.6.5., an open-source 3D freeware (Lebrun, 2018; <https://morphomuseum.com/Pages/morphodig>).

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BIBLIOGRAPHY

- Benammi, M., Adnet, S., Marivaux, L., Yans, J., Noiret, C., Tabuce, R., Surault, J., El Kati, I., Enault, S., Baidder, L., Sadiqi, O., Benammi, M., 2019. Geology, biostratigraphy and carbon isotope chemostratigraphy of the Paleogene fossil-bearing Dakhla sections, Southwestern Moroccan Sahara. *Geological Magazine* 156, 117–132. <https://doi.org/10.1017/S0016756817000851>
- Bohaty, S. M., Zachos, J. C., Delaney, M. L., 2012. Foraminiferal Mg/Ca evidence for Southern Ocean cooling across the Eocene–Oligocene transition. *Earth Planetary Science Letters* 317–318, 251–261. <https://doi.org/10.1016/j.epsl.2011.11.037>
- Lebrun, R., 2018. MorphoDig, an open-source 3D freeware dedicated to biology. 5th International Paleontological Congress (IPC5) – *The Fossil Week*, July 9–13th, 2018 (Paris, France). Abstract volume, 399.
- Marivaux, L., Adnet, S., Benammi, M., Tabuce, R., Benammi, M., 2017a. Anomaluroid rodents from the earliest Oligocene of Dakhla, Morocco, reveal the long-lived and morphologically conservative pattern of the Anomaluridae and Nonanomaluridae during the Tertiary in Africa. *Journal of Systematic Palaeontology* 15, 539–569. <https://doi.org/10.1080/14772019.2016.1206977>
- Marivaux, L., Adnet, S., Benammi, M., Tabuce, R., Yans, J., Benammi, M., 2017b. Earliest Oligocene hystricognathous

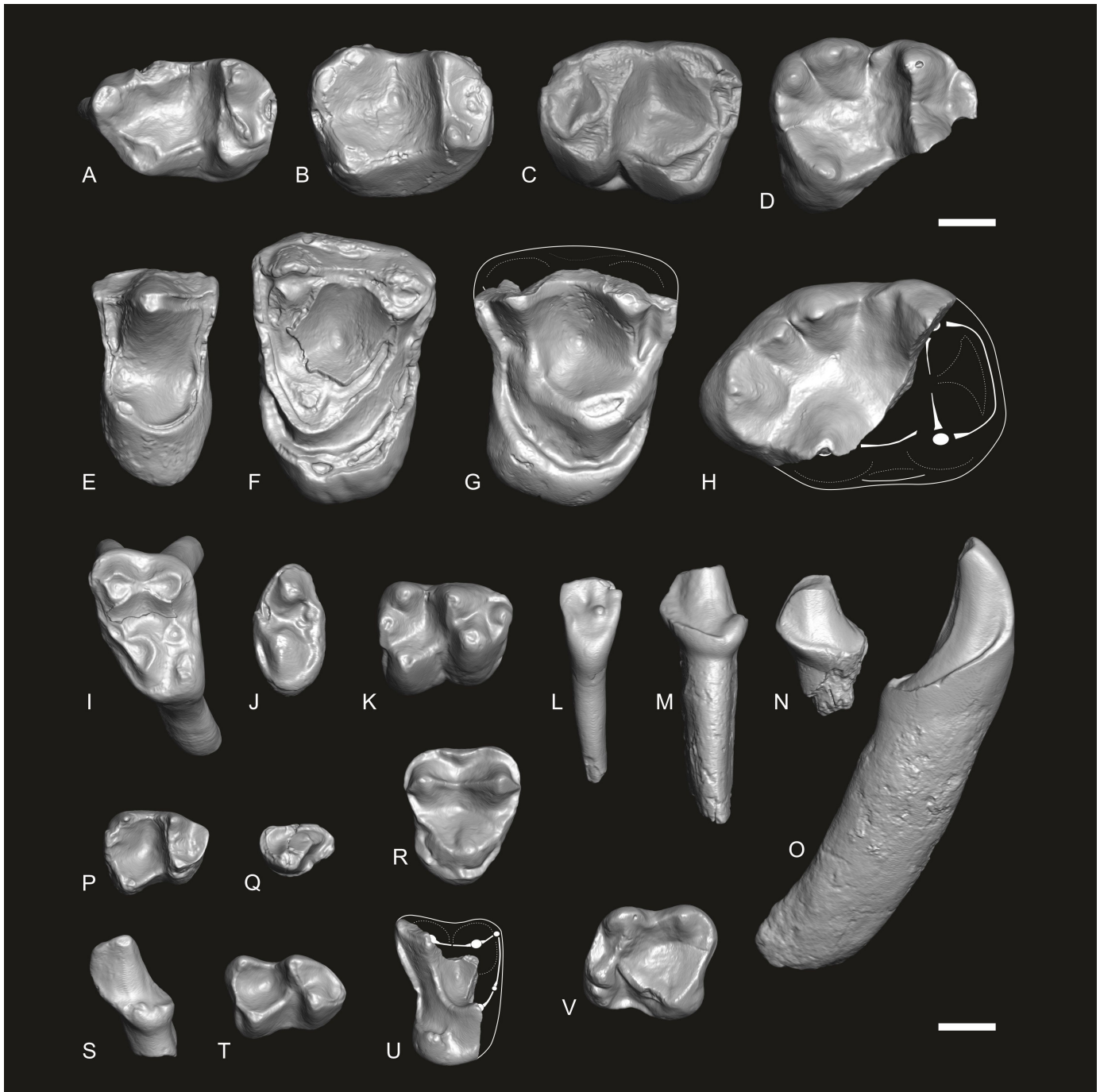


Figure 1. Dental remains of primates (Anthropoidea and Strepsirrhini) from the earliest Oligocene of Dakhla (DAK-Arg C2 and DAK-Pto C2). **A–G**, Oligopithecidae, *Catopithecus* aff. *browni*: DAK-Arg-087, right m3 (A); DAK-Arg-088, right m2 (B); DAK-Arg-089, left m1 (C); DAK-Pto-052, right m1 (mesiobuccally broken; D); DAK-Arg-090, left P4 (E); DAK-Arg-091, left M2 (F); DAK-Pto-053, right M1 (buccally broken; G). **H**, Propliopithecidae, *?Propliopithecus* sp.: DAK-Pto-056, right m3 (fragment of talonid). **I–O**, Parapithecidae, *Abuqatrania* cf. *basiodontos*: DAK-Arg-094, left M1 or M2 (corroded, lacking the enamel cap; I); DAK-Arg-101, left M3 (J); DAK-Arg-093, right m1 (K); DAK-Arg-095, right i1 or i2 (L); DAK-Arg-096, right p2 (M); DAK-Arg-097, right p2 (N); DAK-Arg-092, left c1 (O). **P–Q**, Afrotarsiidae, *Afrotarsius* sp.: DAK-Pto-054, right m1 (P); DAK-Arg-098, left p3 (Q). **R**, Strespirrhini indet., *Orolemur mermozzi*: DAK-Pto-055, right M1 or M2. **S**, Djebelmuridae, cf. *'Anchomomys' milleri*: DAK-Arg-100, right c1. **T–U**, Galagidae Lorisiformes, *Wadilemur* cf. *elegans*: DAK-Arg-099, right m2 (T); DAK-Arg-103, right M1 or M2 (mesially broken; U). **V**, *?Lorisiformes, Orogalago saintexuperyi*: DAK-Arg-102, left m2. Images are renderings of 3D digital models of the fossil specimens, obtained by X-ray micro-computed (μ CT) surface reconstructions (segmented enamel surfaces). The white lines (solid or dashed) drawn on some specimens (G, H, and U) are tentative reconstructions of missing tooth parts, based on homologous dental loci of closely related species. Scale bars = 1 mm.

rodents from the Atlantic margin of Northwestern Saharan Africa (Dakhla, Morocco): systematic, paleobiogeographical and paleoenvironmental implications. *Journal of Vertebrate Paleontology* 37, e1357567. <https://doi.org/10.1080/02724634.2017.1357567>

Marivaux, L., Boivin, M., Adnet, S., Benammi, M., Tabuce, R., Benammi, M., 2019. Incisor enamel microstructure of hystricognathous and anomaluroid rodents from the earliest Oligocene of Dakhla, Atlantic Sahara (Morocco). *Journal of Mammalian Evolution* 26, 373–388. <https://doi.org/10.1007/s10914-017-9426-5>

Marivaux, L., Benammi, M., Baidder, L., Saddiqi, O., Adnet, S., Charruault, A.-L., Tabuce, R., Yans, Y., Benammi, M., 2024. A new primate community from the earliest Oligocene of the Atlantic margin of Northwest Africa: Systematic, paleobiogeographic and paleoenvironmental implications. *Journal of Human Evolution*. <https://doi.org/10.1016/j.jhevol.2024.103548>

Seiffert, E. R., 2012. Early primate evolution in Afro-Arabia. *Evolutionary Anthropology* 21, 239-253. <https://doi.org/10.1002/evan.21335>

Westerhold, T., Marwan, N., Drury, A. J., Liebrand, D., Agnini, C., Anagnostou, E., Barnet, J. S. K., Bohaty, S. M., De Vleeschouwer, D., Florindo, F., Frederichs, T., Hodell, D. A., Holbourn, A. E., Kroon, D., Lauretano, V., Littler, K., Lourens, L. J., Lyle, M., Pälike, H., Röhl, U., Tian, J., Wilkens, R. H., Wilson, P. A., Zachos, J.C., 2020. An astronomically dated record of Earth's climate and its predictability over the last 66 million years. *Science* 369, 1383–1387. <https://doi.org/10.1126/science.aba6853>

Zachos, J. C., Dickens, G. R., Zeebe, R. E., 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* 451, 279–283. <https://doi.org/10.1038/nature06588>