First record of Theropithecus (Cercopithecidae) from the Republic of Djibouti

Denis Geraads, Louis de Bonis

To cite this version:

Denis Geraads, Louis de Bonis. First record of Theropithecus (Cercopithecidae) from the Republic of Djibouti. Journal of Human Evolution, 2020, 138, pp.102686. 10.1016/j.jhevol.2019.102686 . hal-02468836

First record of *Theropithecus* (Cercopithecidae) from the Republic of Djibouti

Denis Geraads [a], [*], Louis de Bonis [b]
[a] CR2P-UMR 7207, CNRS, MNHN, UPMC, Sorbonne Universit_es, CP 38, 8 rue Buffon, 75231 Paris cedex 05, France
[b] PALEVOPRIM-UMR 7262, UFR SFA, Universit_e de Poitiers, 6 rue Michel-Brunet, B^at. 35, TSA 51106, 86073 Poitiers cedex 9, France

Keywords: Primates; Cercopithecidae; systematics; biogeography; Eastern Africa

Abstract: We describe here several specimens of the genus *Theropithecus* from the southern shore of Lake Assal in the Republic of Djibouti; they are the first record of the genus from this country. We assign them to a derived stage of *T. oswaldi*. This identification has implications for the age of the informal 'Formation 1' from this area, which should probably be assigned to the Middle Pleistocene. In addition, the presence of *T. oswaldi* close to the Bab el Mandeb Strait strongly suggests that the species followed this route to India, rather than a more northern one.

1. Introduction

The cercopithecid *Theropithecus*, now restricted to *T. gelada* of the Ethiopian highlands, was one of the most successful primates ever. It is present, and often common, in many late Pliocene to Middle Pleistocene sites of Africa, being especially well-known in East Africa where it is represented in the Pleistocene by the widespread *T. oswaldi*, and by *T. brumpti*, restricted to the Turkana Basin and the Tugen Hills (Jolly, 1972; Eck, 1987; Eck and Jablonski, 1987; Delson, 1993; Jablonski et al., 2008; Jablonski and Frost, 2010; Gilbert et al., 2011). The finds from Djibouti described below add a new country to the range of the genus and have potential implications on its dispersal routes.

In spite of its location at the mouth of the East African Rift System, Djibouti has a limited record of Plio-Pleistocene mammals. The first descriptions of vertebrates were provided by Thomas et al. (1984), followed by Bonis et al. (1984, 1988), Chavaillon et al. (1986), and Harmand et al. (2009). Bonis et al. (1988) provided a detailed account of the fossils found in the Goba'ad plain, the most fossiliferous area of the Republic; they assigned them to the Early and Middle Pleistocene, the most significant find being a *Homo* maxilla (Bonis et al., 1984; Guy et al., 2015). However, they made no mention of the fossils that they had collected further north, on the southern bank of Lake Assal.

Louis de Bonis, Denis Geraads, Françoise Rocroy, and Jean Sudre made a very short survey near the southern bank of Lake Assal in March 1986, but were able to identify two fossiliferous areas (Supplementary information A). One, south-east of Lake Assal (c. 11.53° N, 42.44° E), yielded only a few elephant and hippo remains. The second area, AssalW, extends below their field camp (11.6009° N, 42.3706° E), although the exact coordinates of the fossil finds were not recorded. The sediments clearly belong to what Roger et al. (1974) and Thomas et al. (1984) called 'Formation 1', which also includes their localities MW 196, 197, 201, and 207, defined by Marc Weidmann (in litt.) in the area of Giba Bouyyi. This formation corresponds to what Stieltjes (1980; see Supplementary Online Information (SOM) A) mapped as Plio-Pleistocene clays and conglomerates; it is well exposed on steep slopes below hill 399 (Stieltjes, 1980). It rests upon basalts dated to c. 2.35 Ma (Roger et al., 1974, 1975), and is disconformably overlain by a basalt for which Tapponnier and Varet (1974) provided, without details, an age of at most 0.8 Ma. Roger et al. (1975) reported a polyhedron from MW 197, but obviously neither this isolated artefact nor the *Elephas recki* and *Hippopotamus* cf. *gorgops* reported by Thomas et al. (1984) allow much refinement of the age provided by the underlying basalt. From AssalW, the team led by L. de Bonis collected two partial horn-cores and a mandibular fragment, all definitely identifiable as *Kobus* sp., an antelope usually associated with wet grasslands, plus several *Theropithecus* specimens, described below.

2. Materials and methods

The material, presently housed in the PALEVOPRIM Laboratory, University of Poitiers (UP), includes: UP-AssalW-1, left maxillary fragment with complete but worn P^4, partial, heavily worn P^3 and M^1, and roots of M^2 and M^3; UP-AssalW-2, weathered cranial piece with most of the planum nuchale and left glenoid fossa; UP-AssalW-3 and 4, parts of orbital roof and supra-orbital ridges; UP-AssalW-5, 6, 7, and 8, endocranial fragments, probably from the same individual as AssalW-2; UP-AssalW-9 and 10, left and right maxillary fragments with freshly erupted M^1, showing M^2 and premolar fragments in crypts; UP-AssalW-11, fragment of proximal ulna.

The specimens were measured with callipers to the nearest 1/10 mm and compared for measurements and morphology to most published material.

3. Description and comparisons

AssalW-1 (Fig. 1A, B) is the most informative specimen. The very large partial canine alveolus identifies it as a male; the tooth was at least 16 mm buccolingually wide. The cheek-tooth row is incompletely preserved, but there is no evidence that the curve of Spee was reversed, as is often (but not always) the case in *Theropithecus*. P^4 has the usual *Theropithecus* morphology, with a paracone connected to the protocone by a mesially located crest, and two transverse crests, mesial and distal, bordering two foveae that remain open labially. This tooth is extremely large (Table 1), its breadth being above the range of all other samples except that from Olorgesailie. This extremely large size is confirmed by the measurements of the molars, estimated from the roots by comparison with the large male 067/5608B from Olduvai Bed II; the length of M^2 was certainly close to the maximum length recorded at Olorgesailie. AssalW-1 can unambiguously be identified as a derived *T. oswaldi* by the lack of maxillary ridges (in contrast to *T. brumpti*) and the shortness of the muzzle, as indicated by the steeply ascending maxillo-premaxillary suture, as in the derived subspecies *T. oswaldi leakeyi* from, e.g., Dawaitoli (Frost, 2007). It is longer in early forms (Eck, 1987; Jablonski et al., 2008).

AssalW-9 and 10 (Fig. 1C, D) are certainly from the same individual, smaller than AssalW-1. Fragments of teeth can be seen in the maxilla anterior to the erupted tooth, and no tooth germ was found under the latter, confirming that it is the M^1, while the M^2 is still far from the occlusal level.

AssalW-2 (Fig. 1F, G) is a cranial piece with most of the planum nuchale and left glenoid fossa. It is of moderate size (width across mastoids = 103 mm), similar to that of KNM-ER 41503 (width across mastoids = 104 mm), and is distinctly smaller than KL 337-1 from Bodo (Frost, 2007) and ASB-202 from Asbole (Frost and Alemseged, 2007). In these specimens, the ratio: width across mastoids/length P^3–M^2 is close to 2.45, whereas it would be only c. 1.80 if AssalW-2 were of the same individual as AssalW-1. We therefore believe that AssalW-2 represents a different individual, but it is too large to match the juvenile maxilla AssalW-9/10, suggesting that three different individuals are present in the sample. The axis of the auditory duct is slanting posterolaterally, making an angle of c. 45° with the sagittal plane. Jablonski et al. (2008) observed that it is transverse in old males of *T. oswaldi* from the Upper Burgi Member of the Koobi Fora Fm, in contrast to oblique in *T. brumpti*, but there seems to be much intra-specific variation of this angle. Although weathered, the glenoid fossa displays the shape described by Jablonski (1993, fig.11.3) for *T. oswaldi*, with a mesial expansion of its medial side allowing unilateral anteroposterior translation of the lower jaw. The post-glenoid processes are missing.

AssalW-3 and 4 (Fig. 1E) are parts of the orbital roof and supra-orbital ridges; the supra-orbital ridges are distinctly thicker than those of KNM-ER 1522, KNM-ER 18925 and KNM-ER 41503 from the Upper Burgi Mb, or KNM-ER 1531 from the KBS Mb. They are more similar to those of KNM-ER 5491 (Jablonski et al., 2008, fig. IV.104), KNM-ER 597, KNM-ER 40514, and KNM-ER 40531 from the Okote Mb KL337-1, DAW-VP-1/1 and

HAR-VP-1/1 from Dawaitoli (Frost, 2007), MK4.2006.1 from Makuyuni (Frost et al., 2017, fig.1), or to the Olorgesailie material (KNM-OG 1451, 1452, 1453). The variation in *T. oswaldi* is great, but it may be that the supra-orbital ridges became thicker in the Pleistocene. In front view, the dorsal outline shows a relatively deep, narrow interorbital depression, in contrast to the shallow, broad one of *T. brumpti* (Eck and Jablonski, 1987).

4. Discussion

4.1 Evolutionary stage

From the Pliocene to the Pleistocene, there is no doubt that overall size increased in *Theropithecus*, but evidence that this size increase proceeded in the early Pleistocene is slender. In the Koobi Fora Formation, at the very beginning of the Pleistocene, specimens from the Upper Burgi Member can already reach a very large size (Figs. 2 and 3 show length x width plots of P^4 and M^2 only, but other cheek-teeth tell the same story), not surpassed by those from the later KBS and Okote Members. Size increase resumed thereafter, as specimens from the late early Pleistocene to early Middle Pleistocene of Olduvai Upper Bed II, Kapthurin, Olorgesailie, Melka Kunture, Konso-Gardula, Asbole, Dawaitoli Fm, Makuyuni, Elandsfontein (Hopefield), and Tighennif, usually assigned to the subspecies *T. oswaldi leakeyi*, average larger (Jolly, 1972; Leakey and Leakey, 1973; Delson, 1993; Delson and Hoffstetter, 1993; Leakey, 1993; Frost, 2007; Frost and Alemseged, 2007; Jablonski and Frost, 2010; Frost, 2014; Frost et al., 2017). As first noticed by Jolly (1972), this size increase is mostly restricted to the cheek-teeth; indeed, the canine of AssalW-1 was probably not larger than the largest ones from the Okote Member, in contrast to the molars. Frost (2014) noticed that the transition from *T. oswaldi oswaldi* to *T. oswaldi leakeyi*, the last and most derived subspecies, could be slightly diachronic in the various areas where it occurred, as *T. oswaldi* is already quite large at Konso-Gardula 12, a site dated to c. 1.2 Ma, and latitude and elevation may also have played a role (Delson et al., 2000). However, even if geological age was not the only factor affecting body size, there is no doubt that the AssalW *T. oswaldi* falls within *T. oswaldi leakeyi*. Its very large size, with an estimated body weight close to 100 kg (Delson et al., 2000, fig. 18B) in adult males, even suggests that it belongs to the last stage of the evolution of the lineage.

4.2 Biochronological implications

In AssalW-1, the set of derived features consisting of a short muzzle, very large cheek-teeth, but moderate-size canine, are found only in late representatives of the *T. oswaldi* lineage. Thus, in spite of the limited number of specimens, the evolutionary stage reached by the AssalW *Theropithecus* leaves little doubt as to its age. It is certainly younger than the Okote Member of Koobi Fora or Olduvai upper bed II; the sample size for the other sites is low, but the fact that the M^2 was certainly larger than that of all other specimens, including Asbole, the Dawaitoli Fm, and Makuyuni, all dated to c. 0.6-0.7 Ma, strongly suggests that its age is closer to 0.5 Ma than to 1 Ma.

As mentioned above, the basalts capping the sedimentary exposures of AssalW were first reported to date from c. 0.8 Ma (Tapponnier and Varet, 1974; Roger et al., 1974) but this date must be regarded with caution as no detail has been published on the methods and geographic location of the samples. Zumbo et al. (1994) attempted to date the lava flows of Assal rift margins (Dat'Ali basalts and Adayle trachyte) by $^{40}Ar/^{39}Ar$, but only one of them provided a plateau age of 0.88 Ma; the others were more difficult to interpret, with minimum age estimates of c. 0.4 and 0.5 Ma. So, on the whole there is no major discrepancy between the evolutionary stage of *Theropithecus* and the radiochronologic ages, but we believe that an Early Pleistocene age is unlikely, and thus that an age distinctly earlier than 0.8 Ma can be excluded.

4.3 Ecological implications

AssalW yielded only 12 fossil remains of *Theropithecus* (MNI = at least 2, more probably 3) and three of *Kobus* (MNI = 1), in addition to the two specimens of *Elephas recki* (MNI = 2) and the four *Hippopotamus* cf. *gorgops* (MNI = 2) described by Thomas et al. (1984) from localities MW 196 and 197. Without drawing rash conclusions from such a limited number of fossils, we may tentatively suggest that *Theropithecus* was not a rare component of the mammalian fauna, and that its local environment included a wet grassland, in agreement with its likely grazing food habits. Perhaps this is the reason why it was not found in the earlier Goba'ad deposits (Thomas et al., 1984; Chavaillon et al., 1986; Bonis et al., 1988; Harmand et al., 2009), where the environment was probably drier, because the bovid fauna is dominated by alcelaphins.

4.4 Biogeographic implications

During the African Plio-Pleistocene, fossil *Theropithecus* range from South Africa (where it is last recorded at Elandsfontein [Hopefield]; Delson, 1993; Jablonski and Frost, 2010, and references therein) to North-Western Africa (Algeria: Aïn Jourdel and Tighennif; Morocco: Ahl al Oughlam, Thomas and Oulad Hamida Quarries, Aïn Bahya: Thomas, 1884;

Geraads, 1980; Michel, 1988; Delson and Hoffstetter, 1993; Alemseged and Geraads, 1998). The genus even dispersed to India (Gupta and Sahni, 1981; Roberts et al. 2014) and Spain (Gibert et al., 1995; Ferràndez-Cañadell et al., 2014). At present, its easternmost published African record is from Lee-Adoyta in the Lower Awash Basin of Ethiopia (DiMaggio et al., 2015). It has also been tentatively identified at Buia in Eritrea, c. 1 Ma (Rook et al., 2010) on the basis of a frontal fragment. This identification is likely but we observe that the orbits are less frontally oriented than in other *Theropithecus*. The presence of the genus in Djibouti shows that it extended farther East, on the bank of the Bab el Mandeb Strait. Even if the latter remained open during the whole Pleistocene, there is no doubt that, especially during low sea-level periods, it was not a serious obstacle for many land mammals (Bailey et al., 2007). Further north, a juvenile weathered *Theropithecus* calcaneus was reported from Israel (Belmaker, 2010), but without morphological comparisons; thus, alternative identifications cannot be rejected, especially as the overall shape of the bone (Belmaker, 2010, fig. 2) significantly differs from that of other *Theropithecus* calcanea (e.g., Jablonski et al., 2008, fig. IV-115; SOM B). In any case, the fact that none of the countless Pleistocene European sites (outside Spain) has yielded *Theropithecus* (Patel et al., 2007; Alba et al., 2014) approximates to evidence of absence on the northern shore of the Mediterranean, allowing us to reject a circum-Mediterranean route for the (transient) peopling of Spain. Pending evidence to the contrary, the crossings of both the Gibraltar (Gibert et al., 2016) and Bab el Mandeb Strait by *Theropithecus* are the most parsimonious hypotheses to explain its presence in India and Spain.

References

Alba, D.M., Colombero, S., Delfino, M., Martínez-Navarro, B., Pavia, M., Rook, L., 2014. A thorny question: The taxonomic identity of the Pirro Nord cervical vertebrae revisited. Journal of Human Evolution 76, 92–106

Alemseged, Z., Geraads, D., 1998. *Theropithecus atlanticus* (Thomas, 1884) (Primates: Cercopithecidae) from the late Pliocene of Ahl al Oughlam, Casablanca, Morocco. Journal of Human Evolution 34, 609–621.

Bailey, G.N., Flemming, N.C., King, G.C.P., Lambeck, K., Momber, G., Moran, L.J., Al-Sharekh, A., Vita-Finzi, C., 2007. Coastlines, submerged landscapes, and human evolution: The Red Sea Basin and the Farasan Islands. The Journal of Island and Coastal Archaeology 2, 127–160.

Belmaker, M., 2010. The presence of large cercopithecine (cf. *Theropithecus* sp.) in the Ubeidiya formation (Early Pleistocene, Israel). Journal of Human Evolution 58, 79–89.

Bonis, L. de, Geraads, D., Guérin, G., Haga, A., Jaeger, J.-J., Sen, S., 1984. Découverte d'un hominidé fossile dans le Pléistocène de la République de Djibouti. Comptes rendus de l'Académie des Sciences, Série II, 299, 1097–1100.

Bonis, L. de, Geraads, D., Jaeger, J.-J., Sen, S., 1988. Vertébrés du Pléistocène de Djibouti. Bulletin de la Société Géologique de France 4, 323–334.

Chavaillon, J., Guerin, C., Boisaubert, J.-L., Coppens, Y., 1986. Découverte d'un site de dépeçage à *Elephas recki*, en République de Djibouti. Comptes-rendus de l'Académie des Sciences, série II, 302, 243–246.

Delson, E., 1993. *Theropithecus* fossils from Africa and India and the taxonomy of the genus. In: Jablonski, N.G. (Ed.), *Theropithecus*: The Rise and Fall of a Primate Genus. Cambridge University Press, Cambridge, pp. 157–189.

Delson, E., Hoffstetter, R., 1993. *Theropithecus* from Ternifine, Algeria. In: Jablonski, N.G. (Ed.), *Theropithecus*: The Rise and Fall of a Primate Genus. Cambridge University Press, Cambridge, pp. 191–208.

Delson, E., Terranova, C.J., Jungers, W.L., Sargis, E.J., Jablonski, N.G., Dechow, P.C., 2000. Body mass in Cercopithecidae (Primates, Mammalia): estimation and scaling in extinct and extant taxa. Anthropological Papers of the American Museum of Natural History 83, 1–159.

DiMaggio, E.N., Campisano, C.J., Rowan, J., Dupont-Nivet, G., Deino, A.L., Bibi, F., Lewis, M.E., Souron, A., Werdelin, L., Reed, K.E., Arrowsmith, J.R., 2015. Late Pliocene fossiliferous sedimentary record and the environmental context of early *Homo* from Afar, Ethiopia. Sciencexpress, DOI 10.1126/science.aaa1415

Eck, G., 1987. *Theropithecus oswaldi* from the Shungura Formation, lower Omo basin, south western Ethiopia. In: Les faunes plio-pléistocènes de la basse vallée de l'Omo (Ethiopie). 3, Cercopithecidae de la Formation de Shungura. Cahiers de Paléontologie, Travaux de Paléontologie Est-Africaine, CNRS, Paris, pp. 123–139.

Eck, G., Jablonski, N.G., 1987. The skull of *Theropithecus brumpti* compared with those of other species of the genus *Theropithecus*. In: Les Faunes Plio-Pléistocènes de la Basse Vallée de l'Omo (Ethiopie). 3, Cercopithecidae de la Formation de Shungura. Cahiers de Paléontologie, Travaux de Paléontologie Est-Africaine, CNRS, Paris, pp. 11–122.

Ferràndez-Cañadell, C., Ribot, F., Gibert, L., 2014. New fossil teeth of *Theropithecus oswaldi* (Cercopithecoidea) from the Early Pleistocene at Cueva Victoria (SE Spain). Journal of Human Evolution 74, 55–66.

Frost, S., 2007. Fossil Cercopithecidae from the middle Pleistocene Dawaitoli Formation, Middle Awash Valley, Afar Region, Ethiopia. American Journal of Physical Anthropology 134, 460–471.

Frost, S.R., 2014. Fossil Cercopithecidae of the Konso Formation. In: Suwa, G. (Ed.), Konso-Gardula Research Project, Paleontological Collections: Background and Fossil Aves, Cercopithecidae, and Suidae. University Museum, University Tokyo, Bulletin 47, 43–78.

Frost, S.R., Alemseged, Z., 2007. Middle Pleistocene fossil Cercopithecidae from Asbole, Afar Region, Ethiopia. Journal of Human Evolution 53, 227–259.

Frost, S.R., Saanane, C., Starkovich, B.M., Schwartz, H., Schrenk, F., Harvati, K., 2017. New cranium of the large cercopithecid primate *Theropithecus oswaldi leakeyi* (Hopwood, 1934) from the paleoanthropological site of Makuyuni, Tanzania. Journal of Human Evolution 109, 46–56.

Geraads, D., 1980. La faune des sites à *Homo erectus* des carrières Thomas (Maroc). Quaternaria 22, 65–94.

Gibert, J., Ribot, F., Gibert, L., Leakey, M., Arribas, A., Martinez, B., 1995. Presence of the cercopithecid genus *Theropithecus* in Cueva Victoria (Murcia, Spain). Journal of Human Evolution 28, 487–493.

Gibert, L., Scott, G.R., Scholz, D., Budsky, A., Ferràndez, C., Ribot, F., Martin, R.A., Lería, M., 2016. Chronology for the Cueva Victoria fossil site (SE Spain): Evidence for Early Pleistocene Afro-Iberian dispersals. Journal of Human Evolution 90, 183–197.

Gilbert, C.C., Goble, E.D., Kingston, J.D., Hill, A., 2011. Partial skeleton of *Theropithecus brumpti* (Primates, Cercopithecidae) from the Chemeron Formation of the Tugen Hills, Kenya. Journal of Human Evolution 61, 347–362.

Gupta, V.J., Sahni, A., 1981. *Theropithecus delsoni*, a new cercopithecine species from the upper Siwaliks of India. Bulletin of the Indian geological Association 14, 69–71.

Guy, F., Boistel, R., Lenoir, N., Bonis, L. de, 2015. A Middle Pleistocene fossil hominin maxilla from the Republic of Djibouti (East Africa). Anthropological Science, DOI: 10.1537/ase.150624

Harmand, S., DeGusta, D., Slimak, L., Lewis, J., Melillo, S., Dohmen, I., Omare, M., 2009. Nouveaux sites paléolithiques anciens en République de Djibouti : bilan préliminaire de prospections récentes dans le Bassin du Gobaad, Afar central. Comptes Rendus Palevol 8, 481–492.

Jablonski, N.G., 1993. Evolution of the masticatory apparatus in *Theropithecus*. In: Jablonski, N.G. (Ed.), *Theropithecus*: The Rise and Fall of a Primate Genus. Cambridge University Press, Cambridge, pp. 299–329.

Jablonski, N., Frost, S., 2010. Cercopithecoidea. In: Werdelin, L., Sanders, W.J. (Eds.), Cenozoic Mammals of Africa. University of California Press, San Diego, pp. 393–428.

Jablonski, N.G., Leakey, M.G., Antón, M., 2008. Systematic paleontology of the cercopithecines. In: Jablonski, N.G., Leakey, M.G. (Eds.), Koobi Fora Research Project, The Fossil Monkeys, vol. 6. California Academy of Sciences, San Francisco, pp. 103–300.

Jolly, G.J., 1972. The classification and natural history of *Theropithecus* (*Simopithecus*) (Andrews, 1916), baboons of the African Plio-Pleistocene. Bulletin of the British Museum (Natural History) Geology 22, 1–123.

Leakey, M.G., Leakey, R.E.F., 1973. Further evidence of *Simopithecus*, (Mammalia, Primates) from Olduvai and Olorgesailie. In: Leakey, L.S.B., Savage R.J.G., Coryndon S.C. (Eds.), Fossil Vertebrates of Africa 3. Academic Press; New York, pp. 101–120.

Leakey, M.G., 1993. Evolution of *Theropithecus* in the Turkana Basin. In: Jablonski, N.C. (Ed.), *Theropithecus*: The Rise and Fall of a Primate Genus. Cambridge University Press, Cambridge, pp. 85–123.

Michel, P., 1988. Le gisement de vertébrés pléistocènes d'Ain Bahya (region de Skhirat, Maroc atlantique). Données paléontologiques. Comptes-rendus de l'Académie des Sciences, série II, 307, 435–438.

Patel, B.A., Gilbert, C.C., Ericson, K.E., 2007. Cercopithecoid cervical vertebral morphology and implications for the presence of *Theropithecus* in early Pleistocene Europe. Journal of Human Evolution 52, 113–129.

Roberts, P., Delson, E., Miracle, P., Ditchfield, P., Roberts, R.G., Jacobs, Z., Blinkhorn, J., Ciochon, R.L., Fleagle, J.G., Frost, S.R., Gilbert, C.G., Gunnell, G.G., Harrison, T., Korisettar, R., Petraglia, M.D., 2014. Continuity of mammalian fauna over the last 200,000 years in the Indian subcontinent. Proceedings of the National Academy of Science of the USA, 111, 5848–5853.

Roger, P., Thibault, C., Weidmann, M., Clin, M., 1974. Sur la stratigraphie du Plio-Pléistocène du T.F.A.I. Comptes-rendus de l'Académie des Sciences, Série D, 278, 3291–3293.

Roger, P., Thibault, C., Weidmann, M., 1975. Sur la stratigraphie du Pléistocène dans le centre et le sud du T.F.A.1. In: Pilger A., Rösler, A., (Eds.), Afar Depression of Ethiopia. Schweizerbartsche, Stuttgart, pp. 232–238.

Rook, L., Ghinassi, M., Libsekal, Y., Martínez-Navarro, B., Medin, T., Papini, M., 2010. Stratigraphic context and taxonomic assessment of the large cercopithecoid (Primates, Mammalia) from the late Early Pleistocene palaeoanthropological site of Buia (Eritrea). Journal of Human Evolution 59 (2010) 692–697.

Stieltjes, L., 1980. Carte géologique du rift d'Asal. BRGM, CNRS, Paris.

Tapponnier, P., Varet, J., 1974. La zone de Mak'arrasou en Afar: un équivalent émergé des "failles transformantes" océaniques. Comptes-rendus de l'Académie des Sciences, série D, 278, 209-212.

Thomas, H., Coppens, Y., Thibault, C., Weidmann, M., 1984. Découverte de vertébrés fossiles dans le Pléistocène inférieur de la République de Djibouti. Comptes-rendus de l'Académie des Sciences, série II, 299, 43–48.

Thomas, P., 1884. Sur quelques formations d'eau douce de l'Algérie. Mémoires de la Société géologique de France 3(2), 1–53.

Zumbo, V., Féraud, G., Vellutini, P., Piguet, P., Vincent, J., 1995. First 40Ar/ 39Ar dating on Early Pliocene to Plio-Pleistocene magmatic events of the Afar - Republic of Djibouti. Journal of Volcanology and Geothermal Research 65, 28l–295.

Captions to figures

Figure 1. *Theropithecus* from Djibouti. A−B: AssalW-1, left maxilla with P^4 and roots or fragments of P^3, M^{1-2} in A, left lateral; B, occlusal views. C−D, AssalW-10, left juvenile maxilla with M^1 and erupting M^2 in C, occlusal; D, left lateral views; E, AssalW3, supra-orbital torus, front view; F−G, AssalW2, partial occipital in F, ventral; G, left lateral views.

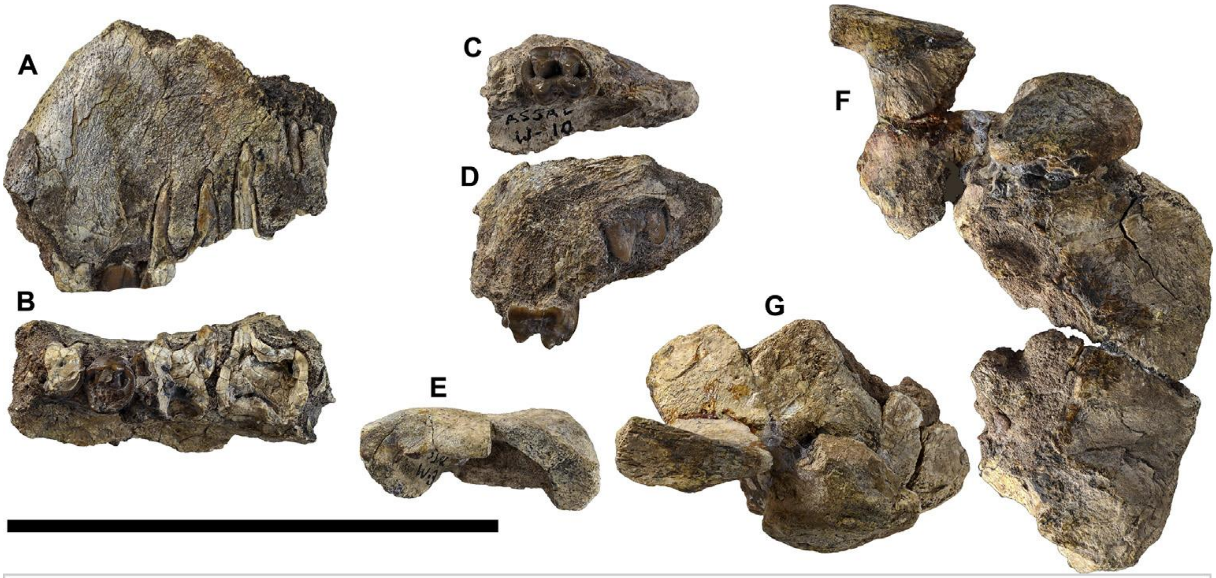
Fig. 2. Length x width plot of *Theropithecus oswaldi* P^4s. The P^4 from Melka Kunture is from Garba XII, a site dated to c. 1 Ma; its great length is due to mesial and distal flaring. The line for Olorgesailie joins the minimum and maximum values, that for Tighennif the minimum, mean, and maximum. Data from Jolly (1972), Leakey and Leakey, 1973; Delson and

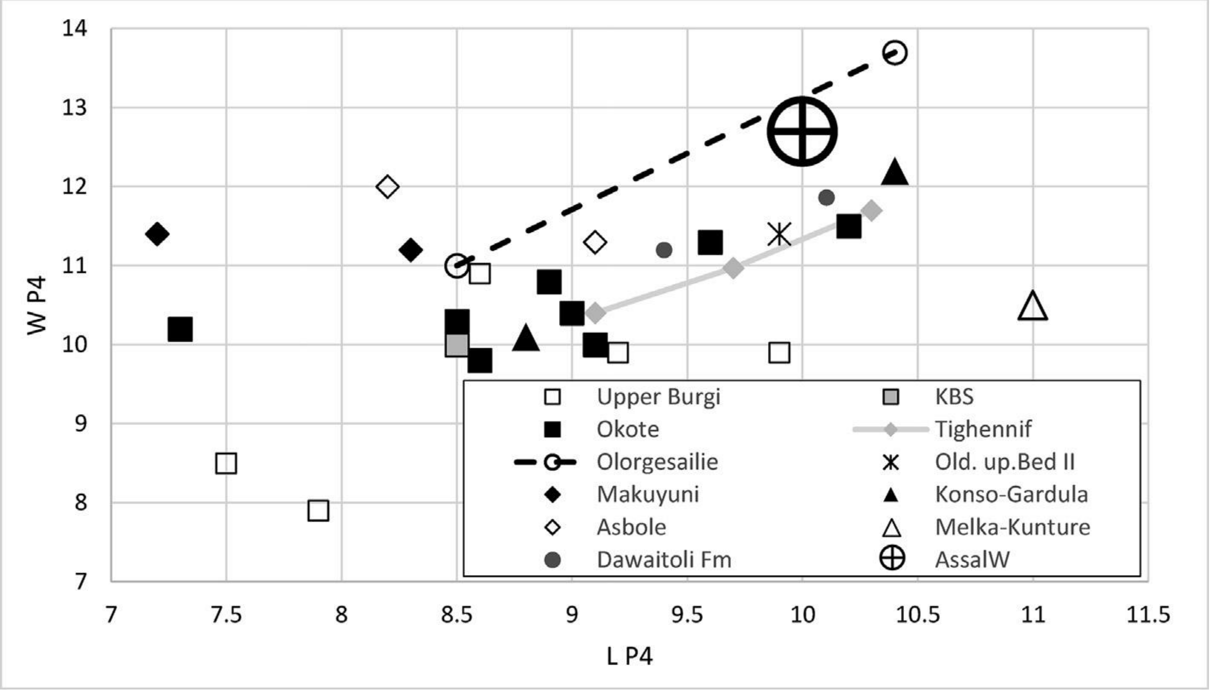
Hoffstetter (1993), Jablonski et al. (2008), Frost and Alemseged (2007), Frost et al. (2017), and the PRIMO database.

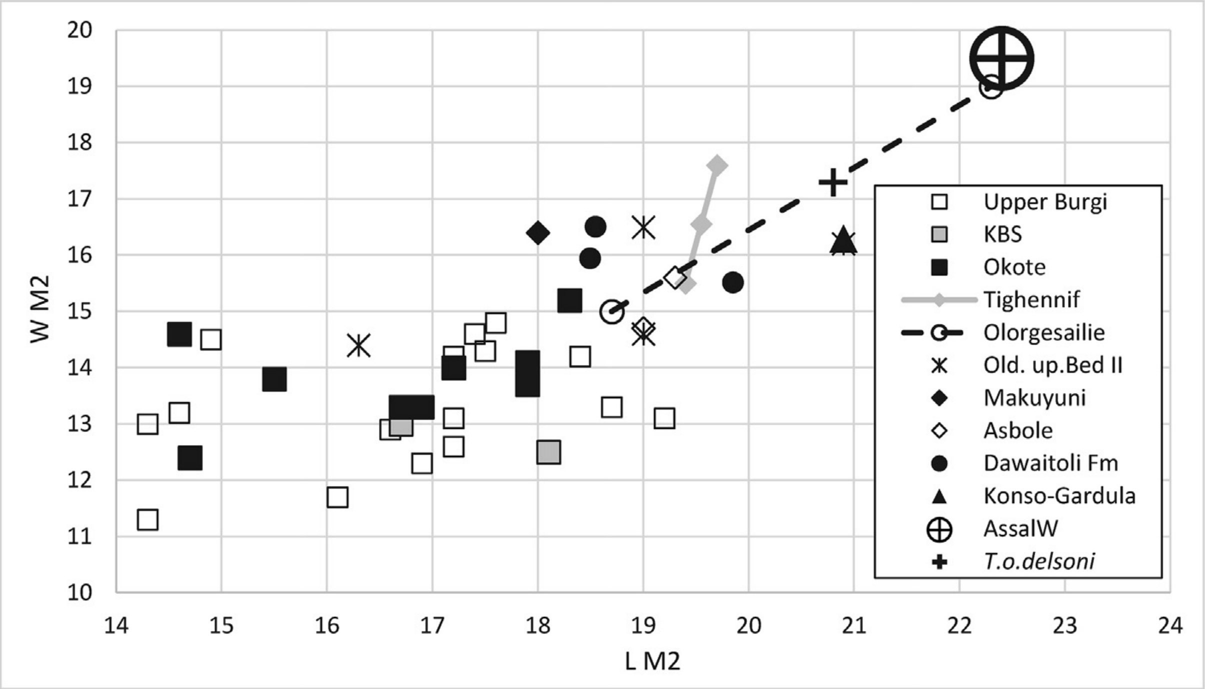
Fig. 3. Length x width plot of *Theropithecus oswaldi* M^2s, and of the least worn tooth of the type maxilla of *T. oswaldi delsoni* from India. The values for AssalW are estimated, but certainly close to the real ones. Sources of data as for Fig 2.

Supplementary information A
Approximate location of AssalW, and detail of the geological map of the Assal Rift (Stieltjes, 1980). [File TheropithecusDjibouti_SupplA.kmz]

Supplementary information B
Upper row: right calcaneum from 'Ubeidiya assigned to cf. *Theropithecus* sp. by Belmaker, 2010 (from Belmaker, 2010, fig.2)
Others rows: calcanei of *Theropithecus oswaldi* from Kenya. From top to bottom: KNM-ER 569, KNM-OG 475 (reversed from the left side) , KNM-OG 958 (reversed from the left side). [File TheropithecusDjibouti_SupplB.tif]


A
B
C
ASSAL W-10
D
E
F
G


14
13
12
11
10
9
8
7
W P4
7
7.5
8
8.5
9
9.5
10
10.5
11
11.5
L P4
□ Upper Burgi
■ Okote
Olorgesailie
◆ Makuyuni
◇ Asbole
● Dawaitoli Fm
KBS
Tighennif
Old. up.Bed II
▲ Konso-Gardula
△ Melka-Kunture
AssalW


W M2
L M2
20
19
18
17
16
15
14
13
12
11
10
14
15
16
17
18
19
20
21
22
23
24
Upper Burgi
KBS
Okote
Tighennif
Olorgesailie
Old. up.Bed II
Makuyuni
Asbole
Dawaitoli Fm
Konso-Gardula
AssalW
T.o.delsoni