Journal of Human Evolution 92 (2016) 50–59

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Reassessment of Olduvai Bed I cercopithecoids: A new biochronological and biogeographical link to the South African fossil record

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ARTICLE INFO

Article history:
Received 13 September 2015
Accepted 6 December 2015
Available online 5 February 2016

Keywords:
Cercopithecid
Papionin
Crania
Gorgopithecus
Baboons
Pleistocene

ABSTRACT

Fossil monkeys have long been used as important faunal elements in studies of African Plio-Pleistocene biochronology, particularly in the case of the South African karst cave sites. Cercopithecoid fossils have been known from Tanzania's Olduvai Gorge for nearly a century, with multiple taxa documented including *Theropithecus oswaldi* and *Cercopithecoides kimeui*, along with papionins and colobines less clearly attributable to species. A small number of large papionin fossils, including a partial male cranium and partial female skull, have been previously identified as an early form of *Papio*, but noted as distinct from extant baboons as well as other fossil *Papio* species. In 2013 we reviewed the Olduvai cercopithecoid material at the National Museum of Tanzania, with a particular focus on the specimens from Beds I–IV. Quantitative and qualitative comparisons of the Olduvai papionins largely confirmed previous observations, with one notable exception. The large papionin taxon from Bed I previously recognized as *Papio* sp. is more properly recognized as *Gorgopithecus major*, a taxon previously known only from South Africa. Features shared between the Olduvai specimens and *G. major* include relatively short and concavo-convex tubular nasals, antero-posteriorly curved upper incisor roots, downwardly curved brow ridges in the midline, and robust zygomatic arches. The recognition of *G. major* at Olduvai Bed I, a well-known horizon with precise radiometric dates, provides an important biochronological and biogeographical link with South African localities Kromdraai A, Swartkrans Member 1 and possibly Swartkrans Members 2–3 and Cooper's A and D.

1. Introduction

Because they are widely present and abundant members of the African Plio-Pleistocene fossil record, cercopithecoid monkeys have played an important role in African biochronology, particularly for many South African localities (e.g., Delson, 1984, 1988; McKee, 1993; McKee et al., 1995; Herries et al., 2009, 2013). Although over one-third of known Plio-Pleistocene cercopithecoid genera are shared between eastern and southern Africa, only five of approximately 45 described species are found in both geographic regions: *Parapapio jonesi*, *Soromandrillus quadratirostris*, *Papio hamadryas*, *Cercopithecoides williamsi*, and *Theropithecus oswaldi*[1] (e.g., Delson,

[1] Harris et al. (1988) recognized cf. *Parapapio whitei* from fragmentary remains that we consider undiagnostic (Frost, 2001, 2007). *Soromandrillus quadratirostris* is found in Angola, not South Africa proper. In this paper, we recognize *T. oswaldi* as an evolving lineage with at least three time-successive chronosubspecies: *T. o. darti*, *T. o. oswaldi*, and *T. o. leakeyi*. See also Leakey (1993), Delson (1993), Frost and Delson (2002), Jablonski (2002), Jablonski and Frost (2010), and Frost et al. (2014).

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http://dx.doi.org/10.1016/j.jhevol.2015.12.003
0047-2484/

Table 1
Qualitative craniodental features found in papionin genera compared to the Olduvai Bed I large papionin specimens.[a]

Taxon	Maxillary fossae	Maxillary ridges in males	Supraorbital tori in males	Muzzle dorsum shape	Nasal bone shape and orientation	Incisor root orientation	Molar enamel
Cercocebus	Present, up to the infraorbital plate to invading the infraorbital plate	Variably present	Not prominent	Variable	Flat to rounded, no anteorbital drop, straight to slightly upturned	Vertical	Non-elevated enamel folding
Dinopithecus	Absent to variably present, very shallow and not clearly defined	–	Prominent, horizontally oriented	Flat to rounded?	Flat to rounded, anteorbital drop, slightly upturned to upturned	Vertical	Non-elevated enamel folding
Gorgopithecus	Present, deeply invading the infraorbital plate	Absent?	Prominent, anteroinferiorly oriented	Peaked	Rounded/tube-shaped, anteorbital drop, slightly upturned to upturned and concavo-convex	Antro-posteriorly curved	Non-elevated enamel folding
Lophocebus	Present, invading the infraorbital plate to deeply invading the infraorbital plate	Variably present	Polymorphic	Variable	Flat to rounded, no anteorbital drop, slightly upturned to upturned	Vertical	Non-elevated enamel folding
Macaca	Absent	Absent	Polymorphic	Variable	Flat to rounded, no anteorbital drop, slightly upturned to upturned	Vertical	Non-elevated enamel folding
Mandrillus	Present, superior to alveoli	Present	Prominent, horizontally oriented	Flat	Flat, anteorbital drop, straight to slightly upturned	Vertical	Non-elevated enamel folding
Papio	Present, up to the infraorbital plate to invading the infraorbital plate	Present	Prominent, horizontally oriented	Flat	Flat, anteorbital drop, slightly upturned to upturned	Vertical	Non-elevated enamel folding
Parapapio	Absent to variably present, very shallow and not clearly defined up to infraorbital plate	Variably present	Not prominent	Variable	Flat to rounded, no anteorbital drop, slightly upturned to upturned and sometimes concavo-convex	Vertical	Non-elevated enamel folding
Pliopapio	Variably present, very shallow and not clearly defined	Absent	Not prominent	Rounded	Rounded, anteorbital drop, upturned	Vertical	Non-elevated enamel folding
Procercocebus	Present, up to the infraorbital plate to invading the infraorbital plate	Present	Not prominent	Variable	Flat to rounded, no anteorbital drop, straight to slightly upturned	Vertical	Non-elevated enamel folding
Soromandrillus	Present, superior to alveoli	Present	Prominent, horizontally oriented	Flat	Flat, anteorbital drop, straight to slightly upturned	Vertical	Non-elevated enamel folding
Theropithecus	Present to variably present, very shallow and not clearly defined to invading the infraorbital plate	Present to variably present	Prominent, horizontally oriented	Variable	Flat, anteorbital drop, slightly upturned to upturned	Vertical	Elevated and complex enamel folding
Oludvai papionin	Present, invading the infraorbital plate to deeply invading the infraorbital plate	Absent?	Prominent, anteroinferiorly oriented	Peaked	Rounded/tube-shaped, anteorbital drop, slightly upturned to upturned and concavo-convex	Antro-posteriorly curved	Non-elevated enamel folding

[a]Dash (–) = State unknown due to lack of preservation. See also Figure 1 and nexus file in SOM for coded character states expressed by each taxon.

1984; Benefit, 1999; Frost, 2007; Jablonski and Frost, 2010; Gilbert, 2013). Among these, only *T. oswaldi* is widely distributed in both regions, leading to a relative dearth of biochronologically significant species aiding in age estimation across Plio-Pleistocene African sites (Delson, 1984; Frost, 2007; Jablonski and Frost, 2010). Here we provide evidence that *Gorgopithecus major*, a genus and species assumed, for the past half-century, to be endemic to South Africa (e.g., Freedman, 1957; Szalay and Delson, 1979; Delson, 1984, 1988; Jablonski, 2002; Jablonski and Frost, 2010), is also present at Bed I Olduvai Gorge, thereby providing an additional time-sensitive link between eastern and southern African hominin-bearing localities.

2. Brief background of fossil monkeys at Olduvai

Fossil cercopithecoids have been known from Olduvai Gorge since the early 20th Century, including well-documented taxa such as *T. oswaldi* and *Cercopithecoides kimeui* (e.g., Remane, 1925[2]; Hopwood 1934; Leakey and Whitworth, 1958; Jolly, 1972; Leakey and Leakey, 1973a,b; 1976; Leakey, 1982). A number of other cercopithecoid specimens are less clearly attributable to specific taxa, but several craniodental fossils from Bed I (male partial cranium OLD/69 S.196, female partial skull FLK NNI 1011, maxillary fragment OLD/69 S.193, and mandibular fragment OLD/61 2968) representing a large papionin taxon were described by Leakey and Leakey (1976) as cf. *Papio* sp. nov., suggesting a new species similar to *Papio* but distinct from other known extant and fossil baboon populations. In general agreement with Leakey and Leakey (1976), Delson (1984) referred to these perplexing Bed I papionin specimens as *?Papio* sp. indet., again indicating that the specimens seemed similar to *Papio*, yet slightly different. A contrasting opinion was expressed by Eck and Jablonski (1984), who attributed the large papionin specimens to *T. oswaldi*, which is common at Olduvai, although the morphological justifications for their reassignments were not specified and the specimens do not display the distinctive *Theropithecus* tooth enamel pattern. Most recently, Frost (2007) linked OLD/69 S.196 to *Papio* as "*Papio* (*Papio*) sp. Olduvai", but did not comment on the other specimens.

In 2013 we reviewed the Olduvai cercopithecoid collection at the National Museum of Tanzania (NMT) as a part of a larger project on African Plio-Pleistocene cercopithecoid systematics and

[2] Remane (1925) reported a well-preserved partial cranium of a juvenile papionin that seems to represent an extant subspecies of *Papio hamadryas*, although its exact identity has never been determined. The specimen was said to derive from Bed IV, which has since been subdivided. Thus its precise horizon and taxonomy are both unclear at this time.