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Evolution of the modern baboon (*Papio hamadryas*): A reassessment of the African Plio-Pleistocene record

Christopher C. Gilbert [a, b, c, d, *], Stephen R. Frost [d, e], Kelsey D. Pugh [b, c], Monya Anderson [e], Eric Delson [b, c, d, f, g, h]

[a] Department of Anthropology, Hunter College of the City University of New York, 695 Park Avenue, New York, NY 10065, USA
[b] PhD Program in Anthropology, Graduate Center of the City University of New York, 365 Fifth Avenue, NY 10016, USA
[c] New York Consortium in Evolutionary Primatology (NYCEP), USA
[d] NYCEP Morphometrics Group, USA
[e] Department of Anthropology, University of Oregon, Eugene, OR 97403-1218, USA
[f] Department of Anthropology, Lehman College of the City University of New York, 250 Bedford Park Boulevard West, New York, NY 10468, USA
[g] Department of Vertebrate Paleontology, American Museum of Natural History, 200 Central Park West, New York, NY 10024, USA
[h] Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona. Edifici ICTA-ICP, Carrer de les Columnes s/n, Campus de La UAB, Cerdanyola Del Vallès, Barcelona 08193, Spain

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ABSTRACT

Baboons (*Papio hamadryas)* are among the most successful extant primates, with a minimum of six distinctive forms throughout Sub-Saharan Africa. However, their presence in the fossil record is unclear. Three early fossil taxa are generally recognized, all from South Africa: *Papio izodi*, *Papio robinsoni* and *Papio angusticeps*. Because of their derived appearance, *P. angusticeps* and *P. robinsoni* have sometimes been considered subspecies of *P. hamadryas* and have been used as biochronological markers for the Plio-Pleistocene hominin sites where they are found.

We reexamined fossil *Papio* forms from across Africa with an emphasis on their distinguishing features and distribution. We find that *P. robinsoni* and *P. angusticeps* are distinct from each other in several cranial features, but overlap extensively in dental size. Contrary to previous assessments, no diagnostic cranio-mandibular material suggests these two forms co-occur, and dental variation at each site is comparable to that within *P. h. ursinus*, suggesting that only one form is present in each case. *P izodi,* however, may co-occur with *P. robinsoni,* or another *Papio* form, at Sterkfontein Member 4.

P izodi appears more primitive than *P. robinsoni* and *P. angusticeps*. *P. robinsoni* is slightly distinct from *P. hamadryas* subspecies in its combination of features while *P. angusticeps* might be included within one of the modern *P. hamadryas* varieties (i.e., *P. h. angusticeps*). No definitive *Papio* fossils are currently documented in eastern Africa until the Middle Pleistocene, pointing to southern Africa as the geographic place of origin for the genus. These results have implications for Plio-Pleistocene biochronology and baboon evolution.

1. Introduction

The savannah baboons of the genus *Papio* are among the most well-known and successful extant primates, with a minimum of six recognizable populations distributed throughout Africa outside of the central forest area, as well as in southern Arabia (Thorington and Groves, 1970; Szalay and Delson, 1979; Jolly, 1993, 2001; Groves, 2001; Frost et al., 2003; Grubb et al., 2003; Fleagle, 2013; see Fig. 1). Despite their evolutionary success and wide distribution across modern African ecological communities, the origins of the genus in the fossil record are not clear. Current molecular and morphological evidence suggests that, among living African papionins, *Papio* is closely related to *Theropithecus*, *Lophocebus*, and *Rungwecebus* (Disotell et al., 1992; Disotell, 1994, 2000; Harris and Disotell, 1998; Fleagle and McGraw, 1999, 2002; Tosi et al., 1999, 2003; Davenport et al., 2006; Gilbert, 2007, 2013; Olson et al., 2008; Burrell et al., 2009; Zinner et al., 2009; Gilbert et al., 2009a, 2011; Roberts et al., 2010), and

* Corresponding author.
E-mail address: cgilbert@hunter.cuny.edu (C.C. Gilbert).

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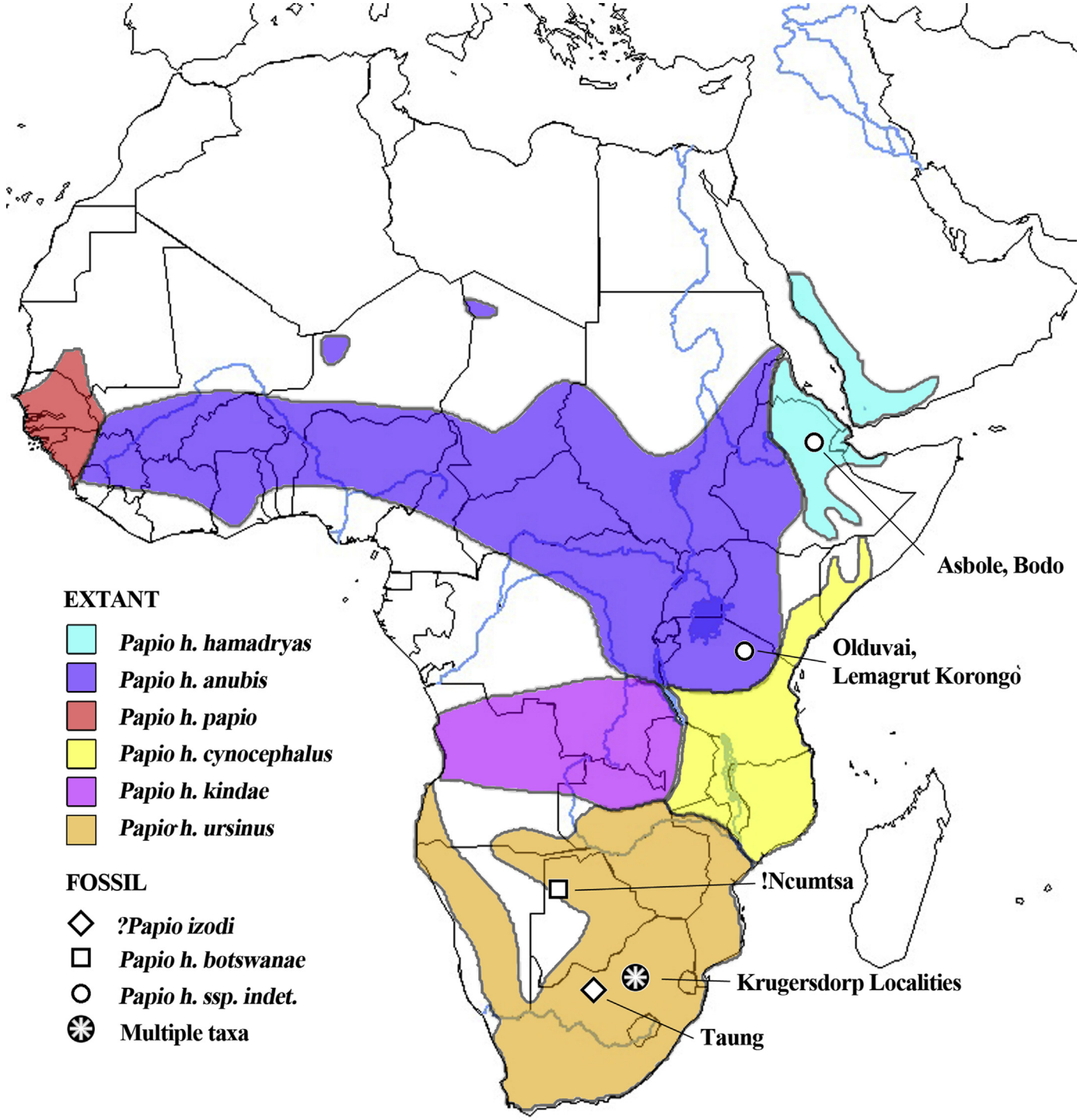

Figure 1. Map of Africa illustrating the geographic distribution of extant and fossil *Papio* populations. Krugersdorp localities include Sterkfontein, Swartkrans, Kromdraai, Bolt's Farm, Cooper's A-D, Gladysvale, Drimolen, Malapa, Haasgat, and Skurweberg.

within this group, the most recent analyses suggest a closer relationship between *Papio* and *Lophocebus,* with *Theropithecus* at the base of this clade (Perelman et al., 2011; Springer et al., 2012; Guevara and Steiper, 2014; Pugh and Gilbert, in press). The position of *Rungwecebus* is controversial, being most recently reconstructed as the sister taxon to *Papio* in molecular studies (Davenport et al., 2006; Olson et al., 2008; Burrell et al., 2009; Zinner et al., 2009; Roberts et al., 2010), yet most similar to *Lophocebus* in morphological comparisons (Jones et al., 2005; Davenport et al., 2006; Singleton, 2009; Singleton et al., 2010; Gilbert et al., 2011a; Gilbert, 2013). Thus, the combination of these data sources implies a close relationship among these three taxa pending additional data.

While *Rungwecebus* is unknown in the fossil record, the earliest specimens of *Theropithecus* are dated to at least 4.2 Ma (Frost, 2001a; Harris et al., 2003; Jablonski et al., 2008; Frost et al., 2014; Frost et al., in revision; Gilbert and Frost, personal obs.). Undoubted *Lophocebus* specimens first appear in the fossil record