



## News and Views

The stem catarrhine *Saadanius* does not inform the timing of the origin of crown catarrhines

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A precise knowledge of the divergence time between Hominoidea (apes and humans) and Cercopithecoidea (Old World monkeys) has been hampered by the paucity of fossils between the early Miocene (23 Ma) and the early Oligocene (30 Ma). The earliest known Old World monkey is represented by *Victoriapithecus macinnesi* from Kenya, dated to 19 Ma (Benefit and McCrossin, 2002; Pilbeam and Walker, 1968), while several potential early hominoid fossils are dated to around 20 Ma, including *Proconsul* at 20–22.5 Ma (Harrison, 2010; Harrison and Andrews, 2009), *Morotopithecus* at 20 Ma (Gebo et al., 1997), and *Ugandapithecus* at 19–20 Ma (Senut et al., 2000). *Kamoyapithecus*, only known from some isolated dentition, dates back to the late Oligocene (23.9–27.8 Ma); however, its phylogenetic position remains controversial and not all authors classify it as a crown catarrhine (Harrison, 2002; Leakey et al., 1995). Based on this evidence in the fossil record, the divergence between hominoids and cercopithecoidea is understood to be older than 20 Mya and most molecular estimates of primate divergences have used this as a calibration point (Chatterjee et al., 2009; Fabre et al., 2009; Hodgson et al., 2009; Raam et al., 2005; Steiper and Young, 2008)

In a recent study, Zalmout et al. (2010) describe a new Oligocene primate from Saudi Arabia, which they claim provides new insights into the time of divergence between apes and Old World monkeys. The newly described fossil, named *Saadanius hijazensis* and dated to ~29 Ma, is inferred to be a stem catarrhine, closely related to living apes and Old World monkeys (crown Catarrhini). According to the authors, this finding indicates an origin for crown Catarrhini after

29 Ma. Here, we argue that this conclusion is unwarranted because stem fossils do not logically provide any temporal information about crown groups.

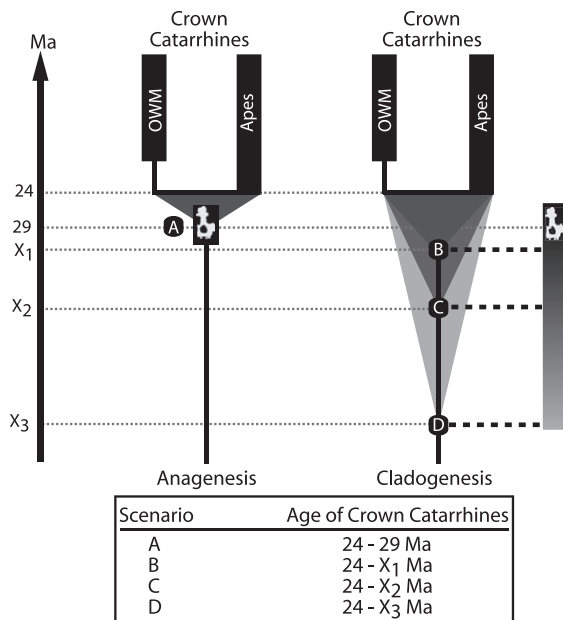
Zalmout et al. (2010) show that *Saadanius* shares derived features with living catarrhines, specifically a tubular ectotympanic, and also shares primitive traits with stem catarrhines (primates related to, but not within, the lineage containing all living catarrhines, e.g., *Aegyptopithecus*). Based on this, the authors conclude that *Saadanius* is a stem catarrhine very closely related to living catarrhines (although their cladistic analyses presented in the supplementary material show the Pliopithecoidea to be more closely related to living catarrhines). The authors then claim that this finding “provides new evidence consistent with a divergence date” between hominoids and cercopithecoidea “after 29–28 Myr ago” (Zalmout et al. 2010, 363).

Zalmout et al. assume that the presence at 29 Ma of a closely related stem taxon such as *Saadanius* indicates that the divergence date of the crown group must be younger. However, it is now widely recognized that the fossil record is only able to provide hard minimum boundaries on divergence times (Benton and Donoghue, 2007; Donoghue and Benton, 2007; Ho and Phillips, 2009; Steiper and Young, 2008). That is, only the oldest known fossils bearing derived characters diagnostic of a clade can be taken as evidence of the presence of that clade at that time. These fossils therefore provide a ‘hard minimum bound’ to the age of the clade and can be used to infer the dates of evolutionary divergences. For example, unlike all other living primates, cercopithecoidea have bilophodont molars. The presence of this derived trait in the fossil *Victoriapithecus*, which first appears 19 Ma, allows us to classify it as a stem cercopithecoidea (Benefit and McCrossin, 2002; Pilbeam and Walker, 1968). It logically follows that the divergence between cercopithecoidea and their nearest living relatives (hominoids) must have occurred prior to 19 Ma.

However, while hard minimum bounds for divergence dates can be supported by fossil evidence, hard maximum bounds – the oldest inferred time for the divergence of two lineages – cannot. This is because a maximum bound implies the absence of a lineage prior to that time, but “the absence of evidence typically does not provide sufficient evidence of absence” (Ho and Phillips, 2009, pp. 370). The presence of stem fossils does not indicate that the crown group has yet to appear. In fact, it is possible that stem taxa can persist long after the appearance of the crown group. For example,

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**Figure 1.** The diagram shows four possible scenarios describing the relationship between *Saadanius* and crown catarrhines (apes and Old World monkeys (OWM)): A) anagenesis; B–D) arbitrary cladogenesis scenarios. For each scenario the range of possible crown catarrhine divergence times are given. The minimum bound is set by the first appearance of a crown catarrhine in the fossil record (*Kamoyapithecus*), while the upper bound is set by the time of divergence between *Saadanius* and the lineage leading to the crown group. It is not possible to determine this divergence time from the fossil record; consequently the various scenarios cannot be distinguished.

the stem catarrhine pliopithecoids persist for perhaps 15–20 Ma after the first appearance of crown fossils (Begun, 2002) as shown in Zalmout et al.'s figure 4. Therefore, stem fossils provide no information about the divergence time of a crown group.

Only a direct ancestor-descendant relationship (anagenesis) between *Saadanius* and the common ancestor of living catarrhines would logically justify the use of this fossil as a hard maximum bound for the divergence between hominoids and cercopithecoids. Only if *Saadanius* is the actual ancestor of both hominoids and cercopithecoids would it necessitate these groups diverging sometime after 29 Ma (Fig. 1a, scenario A). On the other hand, if *Saadanius* represents a side branch sister to crown catarrhines (cladogenesis), as reported in their figure 4, its presence at 29 Ma would not inform the timing of the divergence of the crown group. In fact, the presence of *Saadanius* at 29 Ma can be explained by a divergence from the lineage leading to the crown group any time prior to this (arbitrarily represented with B, C, and D in Fig. 1). Unfortunately, there is no way to distinguish between the anagenesis and the infinite number of cladogenesis scenarios with the fossil evidence.

*Saadanius* is undoubtedly a fascinating discovery that will provide valuable information about the morphology and evolution

of early catarrhines. However, it has no utility in better understanding the timing of the divergence between apes and Old World monkeys.

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## References

- Begun, D.R., 2002. The Pliopithecoidae. In: Hartwig, W.C. (Ed.), *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp. 221–240.
- Benefit, B.R., McCrossin, M.L., 2002. The Victoriapithecidae, Cercopithecoidae. In: Hartwig, W.C. (Ed.), *The Primate Fossil Record*. Cambridge University Press, Cambridge, UK, pp. 241–253.
- Benton, M.J., Donoghue, P.C.J., 2007. Paleontological evidence to date the Tree of Life. *Mol. Biol. Evol.* 24, 26–53.
- Chatterjee, H.J., Ho, S.Y., Barnes, I., Groves, C., 2009. Estimating the phylogeny and divergence times of primates using a supermatrix approach. *BMC Evol. Biol.* 9, 259.
- Donoghue, P.C.J., Benton, M.J., 2007. Rocks and clocks: calibrating the Tree of Life using fossils and molecules. *Trends Ecol. Evol.* 22, 424–431.
- Fabre, P.H., Rodrigues, A., Douzery, E.J.P., 2009. Patterns of macroevolution among Primates inferred from a supermatrix of mitochondrial and nuclear DNA. *Mol. Phylogenet. Evol.* 53, 808–825.
- Gebo, D.L., MacLachy, L., Kityo, R., Deino, A., Kingston, J., Pilbeam, D., 1997. A hominoid genus from the early Miocene of Uganda. *Science* 276, 401–404.
- Harrison, T., 2002. Late Oligocene to middle Miocene catarrhines from Afro-Arabia. In: Hartwig, W.C. (Ed.), *The Primate Fossil Record*. Cambridge University Press, Cambridge, pp. 311–338.
- Harrison, T., 2010. Dendropithecoidae, Proconsuloidea, and Hominoidea. In: Werdelin, L., Sanders, W.J. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 429–469.
- Harrison, T., Andrews, P., 2009. The anatomy and systematic position of the early Miocene proconsulid from Meswa Bridge, Kenya. *J. Hum. Evol.* 56, 479–496.
- Ho, S.Y.W., Phillips, M.J., 2009. Accounting for Calibration Uncertainty in phylogenetic estimation of evolutionary divergence times. *Syst. Biol.* 58, 367–380.
- Hodgson, J.A., Sterner, K.N., Matthews, L.J., Burrell, A.S., Jani, R.A., Raaum, R.L., Stewart, C.B., Disotell, T.R., 2009. Successive radiations, not stasis, in the South American primate fauna. *Proc. Natl. Acad. Sci.* 106, 5534–5539.
- Leakey, M.G., Ungar, P.S., Walker, A., 1995. A new genus of large primate from the late Oligocene of Lothidok, Turkana District, Kenya. *J. Hum. Evol.* 28, 519–531.
- Pilbeam, D., Walker, A., 1968. Fossil monkeys from the Miocene of Napak, North-East Uganda. *Nature* 220, 657–660.
- Raaum, R.L., Sterner, K.N., Noviello, C.M., Stewart, C.B., Disotell, T.R., 2005. Catarrhine primate divergence dates estimated from complete mitochondrial genomes: concordance with fossil and nuclear DNA evidence. *J. Hum. Evol.* 48, 237–257.
- Senut, B., Pickford, A.R., Gommery, D., Kunimatsu, Y., 2000. A new genus of Early Miocene hominoid from East Africa: *Ugandapithecus major* (Le Gros Clark & Leakey, 1950). In: *Sciences de la Terre et des Planetes. Comptes Rendus de l'Academie des Sciences Serie II A*, Vol. 331, pp. 227–233.
- Steiper, M.E., Young, N.M., 2008. Timing primate evolution: lessons from the discordance between molecular and paleontological estimates. *Evol. Anthropol.* 17, 179–188.
- Zalmout, I.S., Sanders, W.J., MacLachy, L.M., Gunnell, G.F., Al-Mufarreh, Y.A., Ali, M.A., Nasser, A.-A.H., Al-Masari, A.M., Al-Sobhi, S.A., Nadhra, A.O., Matari, A.H., Wilson, J.A., Gingerich, P.D., 2010. New Oligocene primate from Saudi Arabia and the divergence of apes and Old World monkeys. *Nature* 466, 360–364.