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The fossil record of camelids demonstrates a late divergence between Bactrian camel and dromedary

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A new compilation of the Old World fossil record of Camelidae and a recent phylogenetic analysis allow a new assessment of the timing of the clade's diversification. Using a recent implementation of the fossilized birth-death process, we show that the divergence between Bactrian camel and dromedary has a peak probability density around 1 Ma and probably occurred less than 2 million years ago. These dates are much younger than molecular estimates, which place the divergence between the dromedary and the Bactrian camel between 4 and 8 million years ago. Calibration problems in molecular dating seem to explain much of this difference.

Key words: Mammalia, Camelidae, phylogeny, divergence time, fossil record, birth-and-death models, Pleistocene, Africa.

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Introduction

Dating the Tree of Life has become an important goal in systematics because timetrees are now routinely used in comparative analyses that study character correlation and hence impact functional biology, in fields as diverse as biomechanics (e.g., Almécija et al. 2015), physiology (e.g., Legendre et al. 2016; Uyeda et al. 2017) and genomics (e.g., Liedtke et al. 2018; Organ et al. 2011). Timetrees are also used to study the evolution of biodiversity through time, using birth-and-death models (Nee et al. 1994; Didier et al. 2017). It is relatively easy to obtain average diversification rates over time (e.g., Höhna et al. 2011), but studying phenomena such as mass extinction events (e.g., Soul and Friedman 2017) and evolutionary radiations (Quental and Marshall 2009), is difficult to do without incorporating fossil data (Rabosky 2009; Sanmartín and Meseguer 2016). Timetrees are even used in conservation biology, through the use of the Phylogenetic Diversity Index (Faith 1992), which allows

a better quantification of biodiversity than taxon counts (Bertrand et al. 2006).

Dating the Tree of Life was initially an essentially paleontological enterprise (Hennig 1981; Laurin 2012), given that fossils provide the only direct evidence of past biodiversity. However, with the development of molecular dating methods, efforts on that front have progressively shifted increasingly towards molecular phylogenetics, which has benefited from the development of many sophisticated methods (see review in Sauquet 2013) that take into consideration variations in molecular evolutionary rates and can use a variety of time constraints with detailed prior information (e.g., Guindon 2018) or incorporate extinct taxa from the fossil record into the analysis (Pyron 2011; Ronquist et al. 2012a, b). These sophisticated developments and the intensive sequencing efforts of the last decades have resulted in such an explosion of the number of available molecular sequences that the limiting factor in dating the Tree of Life accurately is arguably the lack of reliable time constraints,

most of which are derived from the fossil record (e.g., Benton and Donoghue 2007; Parham et al. 2012). Indeed, recent studies suggest that the calibration constraints have great influence over the resulting molecular dates (e.g., Marjanović and Laurin 2007; Warnock et al. 2015) and that insufficient effort has been made to obtain reliable constraints (e.g., Parham et al. 2012; Sterli et al. 2013).

This relative paucity in good dating constraints may explain the frequent discrepancies between molecular and paleontological estimates of clade ages, with molecular ages typically being significantly older than paleontological ages (e.g., Marjanović and Laurin 2007). It is tempting to attribute these discrepancies to the incompleteness of the fossil record, which, after all, only directly provides minimal age estimates. While this may be the right explanation in some cases, this phenomenon is so pervasive that it is unlikely to be the whole answer, and other factors such as variations in generation time can influence molecular rates of evolution and explain some of these discrepancies (e.g., Springer et al. 2017). In any case, palaeontologists often state that some clades must be significantly more recent than their purported molecular estimates, even when taking into consideration the incompleteness of the fossil record (e.g., Fountaine et al. 2005; Wible et al. 2007; Marjanović and Laurin 2008) and uncertainties about the systematic position of some fossils (e.g., Sterli et al. 2013).

To resolve this controversy, improved methods are required to obtain less biased estimates of clade ages based on the fossil record. Such methods should ideally produce probability densities of nodal ages, rather than only the minimal ages that have long been available. Fortunately, important progress has been made on this front recently, using birth-and-death models (Heath et al. 2014; Zhang et al. 2016). Below, we use such a method (Didier and Laurin 2020) to reassess the age of the divergence between two charismatic camelids, the Bactrian camel (*Camelus bactrianus*) and the dromedary (*Camelus dromedarius*), for which fieldwork by several of the authors (DG, WAB, and DR) has produced important new data with well constrained geochronological ages.

Camelidae is an ideal taxon to carry out this study because recent molecular dating studies suggest an age for the Bactrian camel/dromedary divergence of about 4 Ma (Wu et al. 2014; Heintzman et al. 2015), or as much as 8 Ma (Cui et al. 2007). Recently, to calibrate their molecular tree documenting the diversification of wild and domestic populations of Bactrian camels, Ming et al. (2020) assumed a camel/dromedary divergence age of 5.73 Ma based on the TimeTree database (Kumar and Hedges 2011), which summarizes the published molecular ages. However, the fossil record suggests a much younger date of 1–2 Ma (Geraads et al. 2019). Given the two- to eight-fold difference between these two sets (molecular and paleontological) of estimates, an attempt at refining the paleontological estimate of this divergence seems timely. Fortunately, the Neogene fossil record of Camelidae has been well-studied, and several diag-

nostic characters allow us to recognize unambiguously stem-members of various taxa, including those of the Bactrian and the dromedary camels. Our recent phylogenetic analysis of Neogene Old World Camelidae (Geraads et al. 2019) allows us to reappraise the timing of diversification of this clade.

Material and methods

Geraads et al. (2019) produced three equiparsimonious trees using a total of 22 characters, all ordered, analysed using parsimony in TNT (Goloboff et al. 2003; Goloboff and Catalano 2016) and PAUP*4 (Swofford 2003), which provide the topologies that we use to date the evolutionary radiation of Old World Camelini. In addition to *Camelus* species, the analysis included *Paracamelus gigas* Zdansky, 1926, *P. alexejevi* Khaverson, 1950, and *P. alutensis* (Ștefănescu, 1895). The North American *Megacamelus merriami* (Frick, 1921), which is the best-known close relative of Old World camels, was used as an outgroup.

To estimate the timing of the camelid evolutionary radiation, we used a recently-developed computer program (DateFBD) that implements a method that rests on the fossilized birth-and-death model (Didier 2019). Didier and Laurin (2020) provided a method able to compute the distribution of any divergence time of the tree given the speciation (equated with cladogenesis, in this case), extinction and fossilization rates (designated collectively as “rates” below), the tree topology and the (exact) ages of the fossils. In practical applications, the uncertainty on the rates, on the fossil ages and on the tree topologies has to be handled. In the case where there are a great number of equiparsimonious trees (as in Didier and Laurin 2020), the divergence time distributions over all these trees can be summed. Since we have only three equiparsimonious trees in this dataset, we analysed each tree separately. In order to deal with uncertainty on the rates and on the fossil ages, the approach sums the probability densities of nodal ages over all the possible values of rates and fossil ages by using an importance sampling procedure (Didier and Laurin 2020). We assume an improper uniform prior distribution over $[0, \infty]$ for the speciation, extinction and fossilization rates. Each fossil age is entered as a range of possible ages (Table 1; SOM 1 and 2, Supplementary Online Material available at http://app.pan.pl/SOM/app65-Geraads_et_al_SOM.pdf), and we assume a flat distribution within that range to sample each occurrence within that range. The biased density used in the importance sampling procedure weights each combination of possible fossil ages and rates proportionally to the probability of the tree with these fossil ages under the fossilized birth-and-death model with these speciation, extinction and fossilization rates (Didier and Laurin 2020). Sampling this distribution requires a Monte Carlo Markov chain approach and provides the posterior distributions of all the parameters sampled, notably of the speciation, extinction and fossilization rates, which are displayed in Fig. 1.

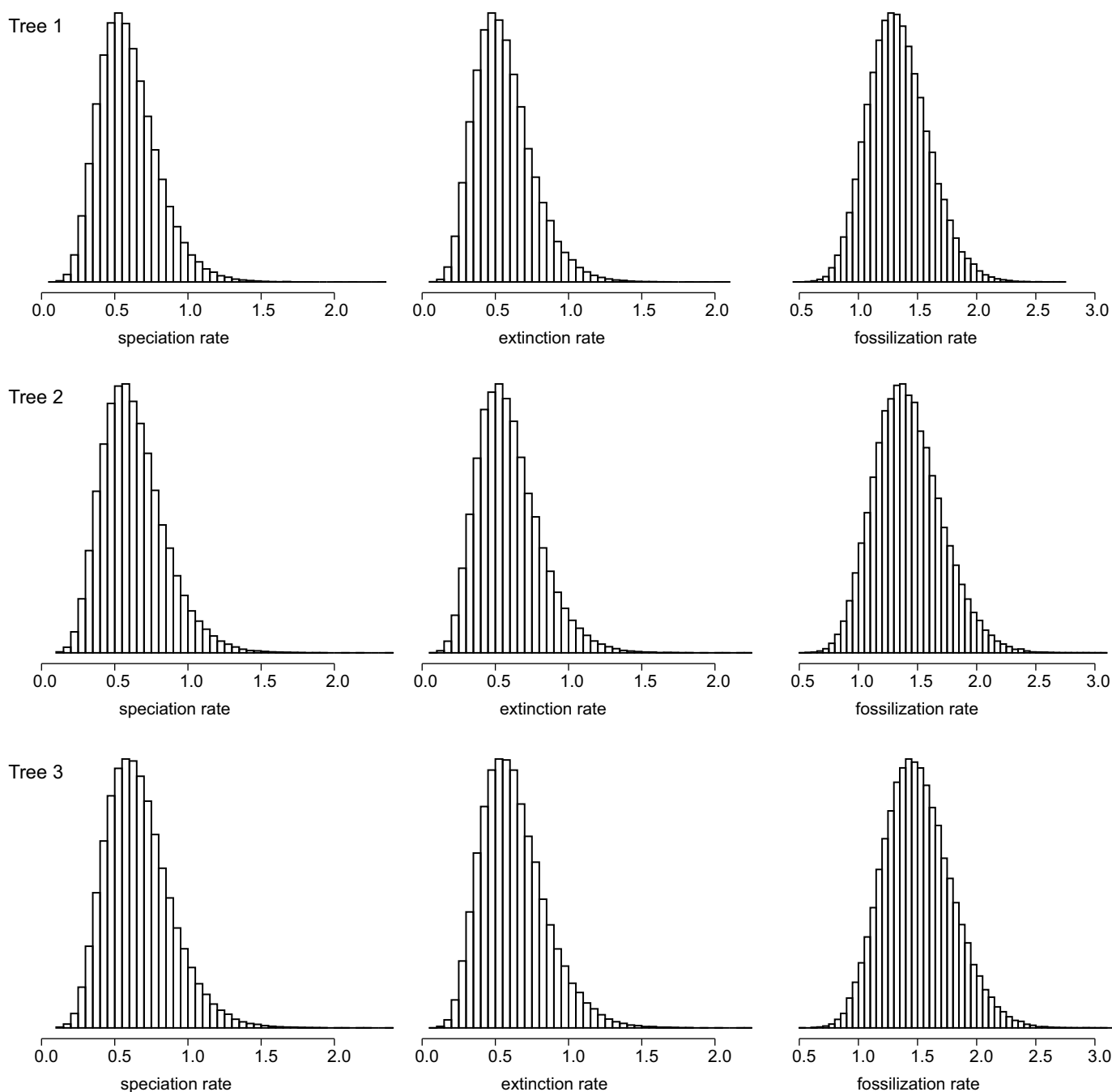


Fig. 1. Probability density histograms of speciation (cladogenesis), extinction and fossilization rates for the three equiparsimonious trees. All rates are in events per lineage and per million years. The height of each box of the plots is proportional to the posterior probability for the corresponding rate to be in the interval delineating its base.

Results

The density of the speciation (cladogenesis) rate peaks at 0.51, 0.55, and 0.57 events per lineage and per My, with 95% confidence intervals of [0.23, 0.98], [0.25, 0.99], and [0.26, 1.11] for trees 1, 2, and 3, respectively. The extinction rate density has modes at 0.47, 0.53, and 0.54 events per lineage and per My, with 95% confidence intervals of [0.22, 0.95], [0.21, 0.94], and [0.23, 1.06] for trees 1, 2, and 3, respectively. The fossilization rate density has peaks at 1.29, 1.35,

and 1.43 fossiliferous horizons per lineage and per My with 95% confidence intervals of [0.88, 1.85], [0.86, 1.84], and [0.95, 2.06] for trees 1, 2, and 3, respectively.

According to our age estimates, most clades have a peak probability density at an age that is compatible with a fairly literal reading of the fossil record (Fig. 2), which suggests that this record is less incomplete than it has been claimed by molecular systematists (Cui et al. 2007; Wu et al. 2014; Heintzman et al. 2015). The *Camelus* crown-group has a peak density at an age just under 1 Ma (0.95 Ma for trees 1

Table 1. List of the records used in “DateFBD”. We list only those records that can be identified to species with good confidence; this explains why a number of *Camelus* records, even if identified to species by other authors, are left aside. Note that several of the dates are only biochronological estimates. The data that are actually used in the analysis (see SOM 1) are in the second column. Notes: ¹ the type-specimen is hardly fossilized; ² identified as *Paracamelus gigas*, but certainly incorrect; ³ species identification likely, but not quite certain; ⁴ the earliest and most reliable record for the living species; ⁵ no associated fauna reported; age probably within the 6.2–3.45 Ma range; ⁶ Plio-Pleistocene (= early Pleistocene in modern terminology) for Teilhard de Chardin and Trassaert (1937), but with little support; contemporaneous with *Dinofelis abeli*, dated by Werdelin and Peigné (2010) 4.5–3.5 Ma; ⁷ Chron C2An; ⁸ stratigraphic origin (“Pontian”) very uncertain; associated with zygolophodont mastodont (i.e., “*Mammuth borsoni*”), but this species survives until well into the Pliocene; ⁹ said to be of middle Pliocene age, but age unsupported—we discard this report; ¹⁰ this occurrence would be earlier than 4 Ma, but Khaveson (1954) clearly stated that the fossil was not found in situ—we discard this report; ¹¹ the purported stratigraphic origin is very doubtful, because there are very few large mammals in the Odessa limestone, and the preservation of the reported fossil suggests a karstic filling rather than a limestone—we discard this report. Abbreviations: AMNH, American Museum of Natural History, New York, USA; CCEC, Centre de Conservation et d’Etude des Collections, Lyon, France; INSAP, Institut National des Sciences de l’Archéologie et du Patrimoine, Rabat, Morocco; KNM, National Museums of Kenya, Nairobi, Kenya; MEUU, Museum of Evolution, Uppsala University, Sweden; MNHN, Muséum National d’Histoire Naturelle, Paris, France; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MTA, Sehit Cuma Dag Natural History Museum, Ankara, Turkey; NHMUK, Natural History Museum, London, UK; NME, National Museum of Ethiopia, Authority for Research and Conservation of Cultural Heritage, Addis-Ababa, Ethiopia; NMNHU, National Museum of Natural History, Kiev, Ukraine; SVCP, Service de Valorisation des Collections de Paléontologie, N’Djamena, Chad; UCBL, Université Claude Bernard, Lyon, France; ZIN, Zoological Institute, Saint Petersburg, Russia.

Taxa, age range, and localities (type locality first)	Age range of the locality (Ma)	Material	Housed in	References	Seen by the authors
<i>Camelus sivalensis</i> Falconer and Cautley, 1836 (2.8–0.6 Ma)					
Pinjor Stage, Upper Siwaliks (India)	2.6–0.6	about 120 cranial and post-cranial specimens	NHMUK	Falconer and Cautley 1836	yes
Boulder Conglomerate (India)	1.7–0.6	partial cranium and other cranial and postcranial elements	AMNH	Colbert 1935	yes
Quranwala (India)	2.8–2.6	cranium	Panjab University, Chandigarh, India	Sahni and Khan 1988	no
Chandigarh, Pinjor Formation (India)	2.6–0.6	partial maxilla and mandible	Panjab University, Chandigarh, India	Gaur et al. 1984	no
<i>Camelus thomasi</i> Pomel, 1893 (1.2–0.5 Ma)					
Tighennif (Algeria)	1.2–0.8	complete cranium, 45 other cranial and postcranial elements	MNHN	Martini and Geraads 2018	yes
Grotte des Rhinocéros (Morocco)	0.6–0.5	isolated teeth, metatarsal	INSAP	Geraads and Bernoussi 2016	yes
<i>Camelus grattardi</i> Geraads, 2014 (2.9–2.2 Ma)					
Omo Shungura Member G4 (Ethiopia)	2.25–2.1	maxilla	NME	Geraads 2014; Rowan et al. 2018	yes
Omo Shungura Member G3 (Ethiopia)	2.25–2.1	partial mandible	NME	Rowan et al. 2018; Geraads et al. 2019	yes
Omo Shungura Member D5 (Ethiopia)	2.5–2.4	phalanx	NME	Geraads et al. 2019	yes
Mille Logya, Seraitu Beds (Ethiopia)	2.9–2.4	partial cranium, isolated teeth, few postcranials	NME	Geraads et al. 2019	yes
West Turkana, Upper Lomekwi (Kenya)	2.7–2.6	mandible	KNM	Harris 1991; Geraads et al. 2019	yes
<i>Camelus knoblochi</i> Nehring, 1901 (0.8–0.01 Ma)					
Luchka, Volga River (Russia)	0.2–0.01	partial cranium ¹	ZIN	Titov 2008	yes
Sjara-osso-gol (China)	0.05–0.03	metatarsal, partial cranium, isolated teeth	MNHN	Boule et al. 1928; Yuan et al. 1983	yes
Wulanmulan (China)	0.07–0.03	maxilla	Ordos Museum, Ordos, China	Dong et al. 2014	no
Lakhti-2 (Tajikistan)	0.8–0.6	no details	?	Titov 2008	no
Koshkurgan (Kazakhstan)	0.4–0.3	teeth and postcranials ²	?	Khisarova 1963	no
Tiraspol (Moldova)	0.8–0.6	no details	?	Titov 2008	no
Russia, Ukraine	0.4–0.1	several crania	various (details in Titov 2008)	Kozhamkulova 1986; Titov 2008	no

Taxa, age range, and localities (type locality first)	Age range of the locality (Ma)	Material	Housed in	References	Seen by the authors
<i>Camelus bactrianus</i> Linnaeus, 1758 (Holocene and Recent)					
various localities	0	17 Recent skulls	MNHN; CCEC; ZIN		yes
Shahr-i-Sokhta (Iran)	0.004–0.003	a few post-cranials ³	?	Benecke 1994; Compagnoni and Tosi 1978	no
Sialk (= Siyalk) (Iran)	0.005–0.004	engravings ³	?	Benecke 1994; Bulliett 1975	no
Anau (Turkmenistan)	0.005–0.004	no details ³	?	Benecke 1994	no
<i>Camelus dromedarius</i> Linnaeus, 1758 (Holocene and Recent)					
various localities		34 Recent skulls	MNHN; CCEC		yes
Al Gharbia (Abu Dhabi)	0.006–0.007	numerous skeletons ⁴	mostly uncollected?	Beech et al. 2009; Marjan Mashkour personal communication 2019	no
<i>Paracamelus gigas</i> Schlosser, 1903 (6.2–3.45 Ma)					
Loc. 102, Henan (China)	? ⁵	partial skeleton	MEUU	Zdansky 1926	no
Gaozhuangian Mammal Age (China)	4.9–3.6	no details	?	Qiu et al. 2013	no
Locs. 11, 17, 26, Shanxi (China)	4.5–3.5 ⁶	partial jaws	Natural History Museum, Tianjin, China	Teilhard de Chardin and Trassaert 1937	no
Venta del Moro, Librilla (Spain) <i>Paracamelus</i> sp.	6.2–5.7	isolated teeth, a few postcranials	MNCN	Morales 1984; Pickford et al. 1995; Pérez-Lorente et al. 2009	no
Kossom Bougoudi (Chad) <i>Paracamelus</i> sp.	6–5	mandible and metapodials	SVCP	Likius et al. 2003	yes
<i>Paracamelus alutensis</i> Ștefănescu, 1895 (3.5–1.5 Ma)					
Milcovul de Jos (Romania)	2.5–1.5	mandible	cast in UCBL	Ștefănescu 1895; Titov 2003	yes (cast)
Khapry-Liventsovka (Russia)	2.5–2.2	more than 200 bones	?	Baigusheva 1971; Titov 2003	no
Fratesti (Romania)	2.5–1.5	partial mandible	Fratesti school ?	Radulescu and Burlacu 1993	no
Oltet Valley (Romania)	2–1.5	no details	?	Titov 2003	no
Dolinskoe (Moldova)	2–1.5	no details	?	Titov 2003	no
Cherevichnoe (Ukraine)	2.5–2.2	«a few findings»	?	Titov 2003	no
Sarikol Tepe (Turkey)	2.5–2.3	maxilla, partial mandible, metapodials	MTA	Kostopoulos and Sen 1999	no
karstic fillings of the Odessa catacombs (Ukraine)	3.5–3	partial mandible	NMNHU	Logvynenko 2001; Nagel et al. 2004	no
<i>Paracamelus alexjevi</i> Khaverson, 1950 (6–3 Ma)					
karstic fillings of the Odessa catacombs (Ukraine)	3.5–3 ⁷	abundant material, but fragmentary and partly reconstructed	Paleontological Museum, Odessa, Ukraine	Khaverson 1954; Logvynenko 2000; Nagel et al. 2004	no
Cherkassy (Ukraine)	6–3 ⁸	partial mandible	?	Svistun 1971	no
Kagul district (Moldova)	? ⁹	partial cranium	?	Svistun et al. 1989	no
Pavlodar (Kazakhstan)	? ¹⁰	phalanx	?	Khaverson 1954; Titov and Tesakov 2013	no
Odessa limestone (Ukraine)	? ¹¹	partial mandible	Geological Institute, Russian Academy of Sciences, Moscow, Russia	Titov and Logvynenko 2006	no
<i>Megacamelus merriami</i> (Frick, 1921) (6.7–4.8 Ma)					
Mount Eden Formation, Keams Canyon, Santee and Devil's Nest (Hemphillian 3–4; USA)	6.7–4.8	abundant cranial and postcranial material	AMNH	Harrison 1985; Honey et al. 1998	yes

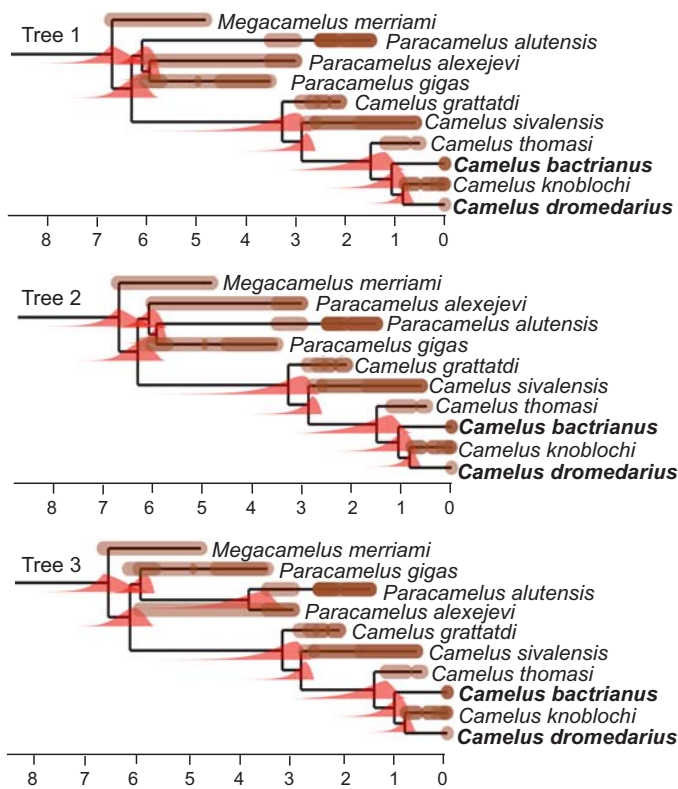


Fig. 2. Time-calibrated equiparsimonious trees. At each node, the probability density computed by diversification is shown (in red, all displaying a left skew). The age of each fossil record (in million years) is shown as a brown bar along each branch, which extends from the oldest to the youngest plausible age for each record. Darker shades represent overlapping possible age ranges, whereas brown dots represent very well-dated fossils. Extant taxa are in bold. A monophyletic *Camelus* is diagnosed by the loss of p3 and a smaller P3. The *Paracamelus* clade is diagnosed by a long muzzle. *Camelus grattardi* lacks derived characters of other representatives of the *Camelus* clade, the paraglenoid process, a shallower infra-orbital shelf, an oblique ascending ramus of the mandible, a thickened corpus, a broader P4 relative, and long ligament scars on the phalanges. The position of the poorly studied *Camelus knoblochi* relative to extant forms rests only on the morphology of the choanae.

and 2 and 0.93 Ma for tree 3), and its density dwindles to near 0 between 2 and 3 Ma (95% confidence intervals are [1.82, 0.75] for trees 1 and 2 and [1.73, 0.74] for tree 3; Fig. 3). The more inclusive *Camelus* clade (whose oldest members are all extinct) has a peak density at 3. Ma with 95% confidence interval [4.78, 2.77] for trees 1 and 2 and at 2.97 Ma with 95% confidence interval [4.57, 2.75] for tree 3. The probability densities dwindle to near 0 around 6.5 Ma for the three trees (Fig. 3).

Discussion

The relatively narrow probability densities for the rates (Fig. 1) suggest that our results are fairly reliable. All the simulations passed the convergence tests implemented in the coda package with effective sizes above 10 000 samples (Plummer et al. 2006). Estimated speciation and extinc-

tion rates for Neogene camelids are about twice as high as those obtained by Didier and Laurin (2020) on Permo-Carboniferous amniotes, whereas the fossilization rates are about 40 times as high. The latter discrepancy presumably reflects the much greater collection effort in Neogene sediments than in those of the late Paleozoic, as well as their greater availability (Bouysse et al. 2000). Whether the more modest discrepancies in speciation and extinction rates reflect genuine differences in evolutionary dynamics between Permo-Carboniferous amniotes and Neogene camelids is less certain because this is only the second empirical application of our method (the first one being found in Didier and Laurin 2020), but the simulations performed so far (Didier and Laurin 2020) suggest that rate estimates should improve with stratigraphic sampling density. This suggests that the rates for Neogene camelids should be reliable, despite the relatively low number of sampled taxa.

The differences in rates and ages between the three trees are modest, especially between trees 1 and 2. The slightly greater differences between results of the third tree and those of the other two trees can probably be explained by the fact that tree 3 places *Paracamelus gigas*, which is geologically older than the two other species of *Paracamelus*, in a basal position within *Paracamelus*. This results in younger ages for *Paracamelus*, for the node subtending *Paracamelus* and *Camelus*, and even for the *Camelus* crown. Nevertheless, these differences remain subtle and do not affect our main conclusions because the molecular ages with which we can compare our results differ greatly from our estimates.

This estimated divergence date between the lineages leading to both extant *Camelus* species (0.94 Ma) is only slightly older than the minimal age of 0.6–0.8 Ma that we had recently reported (Geraads et al. 2019); it is in fairly

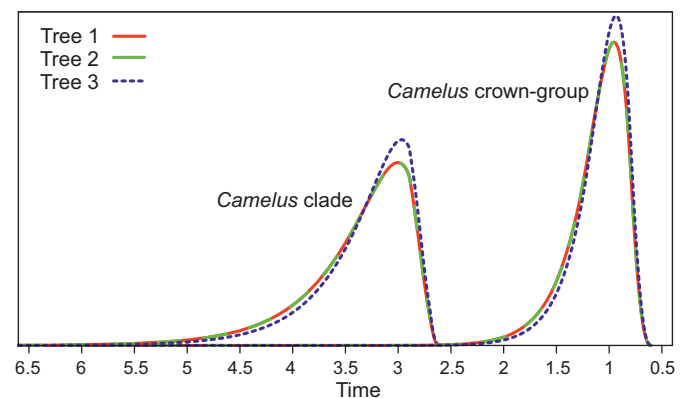


Fig. 3. Probability density of the age of crown (extant) *Camelus* and of *Camelus* itself (including older stem-species, namely *Camelus grattardi*, *Camelus sivalensis*, and *Camelus thomasi*) for the three equiparsimonious trees. These were computed by DateFBD (Didier 2019). The curves for trees 1 (red) and 2 (green) overlap (curve with long dashes). Only tree 3 (blue) yields a different probability density. The probability for a divergence time to be in a given time interval is proportional to the surface below its probability density curve for this interval of time (it is exactly the probability of being in the interval if one assumes that the total surface below the probability density curve is equal to one).

good agreement with the discovery in Syria at 450 ky of a camel said to be intermediate (unfortunately, no details have been published yet) between *C. bactrianus* and *C. dromedarius* (Martini et al. 2015). Indeed, the 95% confidence intervals on our estimate of the divergence date between Bactrian camel and dromedary extends until 0.75 Ma, and after this divergence, the phenotypes of both lineages would have diverged gradually. Back at 0.5 Ma, the phenotypes of both lineages should be markedly closer to each other than today. By contrast, our age estimate is much more recent than the estimates provided by molecular dating: c. 4.4 Ma according to Wu et al. (2014) using the whole genome, and c. 4.1 Ma by Heintzmann et al. (2015), based partly on the genome of the late Middle Pleistocene American *Camelops*. Based on mtDNA sequence, Cui et al. (2007) even suggested that this divergence occurred around 8 Ma, which is before the Camelidae immigrated into the Old World, where its earliest securely dated record is at Librilla, Spain, c. 6.3 Ma (Alberdi et al. 1981). Our results strengthen the conclusions of Geraads et al. (2019) and are incompatible with the molecular ages mentioned above. However, these strong discrepancies with recent molecular estimates should be explained.

Cui et al. (2007) calibrated their tree using two calibration constraints: a cow/pig divergence, set at 65 Ma, and a mouse/rat divergence, set at 14 Ma. Both constraints deserve comments. The first (cow/pig divergence) was taken from Springer et al. (2003), a molecular study of placental mammal diversification. As such, that constraint is a secondary calibration, a practice that has been criticized (Shaul and Graur 2002) for adding uncertainty that is not necessarily incorporated into subsequent estimates. This is unfortunately the case here, to the extent that Cui et al. (2007) do not report credibility or confidence intervals for the estimated ages. In addition, a cow/pig divergence at 65 Ma implies a substantial cryptic biodiversity of Mesozoic placentals, which analyses of the fossil record refute (Davies et al. 2017). The other calibration, between mouse and rat, was set at an older age than suggested by Benton and Donoghue (2007: table 1), who suggested an age of 11–12.3 Ma, and Kimura et al. (2015), who suggested an age of about 12 Ma. More importantly, the phylogenetic analysis of Patnaik (2014), which is probably the most thorough paleontological study of the *Mus/Rattus* divergence, suggests an even younger minimal age of only 7.3 Ma. However, comparisons between the results of Patnaik (2014) and Kimura et al. (2015) are complicated by differences in taxonomic sample and topology. Nevertheless, it seems fair to state that the fossil record indicates that the minimal age of the *Mus/Rattus* divergence is less than 14 Ma, given that Patnaik (2014) and Kimura et al. (2015) agreed on this point. Thus, Cui et al. (2007) probably overestimated the age of the mouse/rat divergence by 15–90% (an admittedly large bracket that reflects considerable uncertainty in the implications of the murine fossil record). In addition, the assumption of a constant rate of change was rejected for that dataset (Cui et al.

2007: 5), and all the problems evoked here, combined with the lack of confidence or credibility intervals, may explain much of the discrepancy between the age of 8 Ma reported by Cui et al. (2007) and our estimate.

The study by Wu et al. (2014) similarly displays calibration problems. It used four constraints: *Homo sapiens/Mus musculus* (61.5–100.5 Ma), *Canis lupus familiaris/Equus caballus* (62.3–71.2 Ma), *Bos taurus/H. sapiens* (95–113 Ma), all from Benton and Donoghue (2007), and *H. sapiens/Monodelphis domestica* (124.3–138.4 Ma), reportedly from a web site (<http://www.fossilrecord.net/>) that seems to no longer work. The three constraints taken from Benton and Donoghue (2007) appear much too old. Like the constraints used by Cui et al. (2007), they imply a substantial cryptic biodiversity of Mesozoic placentals, which are refuted by the analyses of Davies et al. (2017). They also rely on taxonomic affinities of mostly fragmentary Cretaceous mammals that have been refuted by subsequent research. For instance, the *Bos taurus/H. sapiens* divergence calibration set at 95–113 Ma relies on the age of *Bobolestes*, *Paranyctoides*, and *Batodon*, which Benton and Donoghue (2007: 34) suggest fit within this divergence. However, the phylogenetic analyses of Wible et al. (2007), O’Leary et al. (2013) and Carrillo and Asher (2017) placed these taxa on the placental stem and suggested that crown-placentals were known only from the Cenozoic. These problems with calibration constraints are serious enough to cast doubt about the reliability of the ages reported by Wu et al. (2014).

Heintzmann et al. (2015) used three constraints. One is a prior on the root of crown-group Artiodactyla placed at 59 Ma with a lognormal distribution, with 90% of the prior distribution placed between 52.5 and 66 Ma, based on the first occurrence of *Himalayacetus* in the fossil record. Benton et al. (2015: 67) reported that *Himalayacetus* was known only from a partial dentary and two molars and that it may be related to ambulocetids or pakicetids, so this constraint appears to be correct. Another constraint is a normal prior with a mean of 17.5 Ma and a standard deviation of 1.52 Ma for the divergence between Camelini and Lamini, based on the first appearance of *Aepycamelus* (Lamini), and this seems to reflect the current consensus (Gasparini et al. 2017). The third constraint is a prior with a mean of 4.4 Ma and a standard deviation of 1.43 Ma for the *Camelus bactrianus/Camelus dromedarius* divergence taken from Wu et al. (2014), which is subject to the caveats mentioned above. Thus, while two of the three constraints appear to be appropriate based on current knowledge, the node of interest (divergence between *C. bactrianus* and *C. dromedarius*) had been constrained on the age obtained by Wu et al. (2014), which is most likely inflated, as explained above.

To sum up, the differences between our paleontological results and those of recent molecular studies do not appear to result from conflicting signals from these two types of data. Rather, they result from a suboptimal use of the fossil record to constrain molecular dating analyses. This is not surprising because the paleontological literature is rich and

widely scattered. We suggest that future endeavors in this field would be best undertaken by research groups incorporating both molecular systematists and paleontologists, as has been done for some of the best works in this field (e.g., Ronquist et al. 2012a).

Conclusions

Our reasonably well-constrained divergence dates (Figs. 2, 3) show that the recently-developed paleontological dating method based on the fossilized birth-death process (Didier and Laurin 2020) works well with datasets of a modest size (here, with 10 species) and in clades with a moderately-rich fossil record (here, a total of 38 stratigraphic occurrences). Thus, this method could profitably be used in a wide variety of taxa with a reasonably rich fossil record and a sufficiently complex morphology that allows placing fossils in a phylogeny. Such taxa range in time at least from the Cambrian (e.g., trilobites) to the present. An extensive use of such methods in palaeontology should significantly improve the accuracy and reliability of our calibration of the Tree of Life, both by directly estimating divergence dates of clades that are well-represented in the fossil record, and through the use of the resulting probability density distributions of divergence times to better constrain molecular clocks of clades with a poor fossil record. This should significantly enhance the integration of palaeontologists into the rapidly-growing community of systematists involved in dating the Tree of Life.

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