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Evolutionary biology

Forest refugia in Western and Central Africa as 'museums' of Mesozoic biodiversity

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The refugial speciation model, or 'species pump', is widely accepted in the context of tropical biogeography and has been advocated as an explanation for present species distributions in tropical Western and Central Africa. In order to test this hypothesis, a phylogeny of the cryptic arachnid order Ricinulei, based on four nuclear and mitochondrial DNA markers, was inferred. This ancient clade of litter-dwelling arthropods, endemic to the primary forests of Western and Central Africa and the Neotropics, might provide insights into the mode and tempo of evolution in Africa. Twenty-six African ricinuleid specimens were sampled from eight countries spanning the distribution of Ricinulei on the continent, and analysed together with Neotropical samples plus other arachnid outgroups. The phylogenetic and molecular dating results suggest that Ricinulei diversified in association with the fragmentation of Gondwana. The early diversification of *Ricinoides* in Western and Central Africa around 88 (± 33) Ma fits old palaeogeographical events better than recent climatic fluctuations. Unlike most recent molecular studies, these results agree with fossil evidence, suggesting that refugia may have acted as 'museums' conserving ancient diversity rather than as engines generating diversity during successive episodes of climatic fluctuation in Africa.

1. Introduction

The existence of forest refugia is broadly accepted in tropical biogeography, because there is ample evidence for forest fragmentation linked to past climatic change in temperate and tropical regions [1,2]. Two different hypotheses have been advanced regarding the role of refugia in shaping the current biodiversity of tropical Africa. The refugial speciation model [3], or 'species pump', invokes genetic differentiation between allopatric populations, fragmented and trapped in refugia by the expansion of savannah during Quaternary glacial maxima [4]. This hypothesis predicts the origin of most rainforest species to be relatively recent [5]. On the other hand, past climatic changes could have depleted rather than augmented biodiversity, suggesting that refugia might have acted as 'museums' for ancient lineages, and divergence between sister species might pre-date climatic fluctuations [6]. Whereas fossil evidence for plants has long suggested an ancient diversity followed by cycles of extinction owing to climatic fluctuation [7], most molecular studies (see the electronic supplementary material,

Table 1. Tissue sample numbers, provenance data, GenBank accession numbers and voucher repositories for Ricinulei and outgroup taxa from which DNA sequence data were generated for the present study. COI, cytochrome c oxidase subunit I.

MCZ voucher	repository	latitude	longitude	ID	country	18S rRNA	28S rRNA	12S rRNA	COI
DNA102704	MCZ	-3.68333	-70.25000	<i>Cryptocellus peckorum</i> Platnick and Shadab, 1977	Colombia	JX951342	JX951355	—	—
DNA102711	MCZ	-4.12000	-69.92222	<i>C. peckorum</i> Platnick and Shadab, 1977	Colombia	JX951320	JX951357	JX951380	—
DNA102712	MCZ	-4.04472	-69.98972	<i>C. peckorum</i> Platnick and Shadab, 1977	Colombia	JX951321	JX951358	JX951381	—
DNA102713	MCZ	-4.12028	-69.97528	<i>C. peckorum</i> Platnick and Shadab, 1977	Colombia	JX951322	JX951359	JX951382	JX951406
DNA102701	MCZ	9.67167	-83.02500	<i>Cryptocellus</i> sp.	Costa Rica	JX951317	JX951354	JX951377	JX951404
DNA102710	MCZ	-4.37889	-69.99028	<i>Cryptocellus</i> sp.	Colombia	JX951319	JX951356	JX951379	—
DNA103735	MCZ-IZ-80067	8.40667	-83.32833	<i>Cryptocellus</i> sp.	Costa Rica	JX951327	JX951364	JX951387	JX951410
DNA103733	MCZ	15.11440	-89.68047	<i>Pseudocellus</i> sp.	Guatemala	JX951325	JX951362	JX951385	—
DNA103734	MCZ	15.58333	-86.66833	<i>Pseudocellus</i> sp.	Honduras	JX951326	JX951363	JX951386	JX951409
DNA103736	MCZ-IZ-79799	15.71566	-92.93817	<i>Pseudocellus</i> sp.	Mexico	JX951328	JX951365	JX951388	JX951411
DNA102708	AMNH	6.25039	1.04039	<i>Ricinoides atewa</i> Naskrecki, 2008	Ghana	JX951318	—	JX951378	JX951405
DNA105884	MRAC 225977	7.66667	-8.43333	<i>Ricinoides</i> cf. <i>afzelii</i>	Guinea	JX951338-9	—	—	—
DNA104741	MCZ	3.64538	11.29033	<i>Ricinoides</i> cf. <i>olounoua</i>	Cameroon	JX951329	—	JX951389	JX951412
DNA104742	MCZ	3.64447	11.29107	<i>Ricinoides</i> cf. <i>olounoua</i>	Cameroon	JX951330	—	JX951390	JX951413
DNA104744	MCZ	3.66153	11.30262	<i>Ricinoides</i> cf. <i>olounoua</i>	Cameroon	JX951332	JX951367	JX951391	JX951415
DNA104745	MCZ	3.66195	11.30025	<i>Ricinoides</i> cf. <i>olounoua</i>	Cameroon	JX951333	—	JX951392	JX951416
DNA105538	MCZ	3.64513	11.29078	<i>Ricinoides</i> cf. <i>olounoua</i>	Cameroon	JX951336	—	JX951395	JX951419
DNA102691	AMNH LP4658	12.08156	-14.80103	<i>Ricinoides feae</i> (Hansen, 1921)	Guinea-Bissau	JX951312	JX951349	JX951373	JX951399
DNA102692	AMNH LP4660	12.08156	-14.80103	<i>R. feae</i> (Hansen, 1921)	Guinea-Bissau	JX951313	JX951350	JX951374	JX951400
DNA102693	AMNH LP4661	12.08156	-14.80103	<i>R. feae</i> (Hansen, 1921)	Guinea-Bissau	JX951314	JX951351	JX951375	JX951401
DNA102694	AMNH LP4662	11.88442	-14.83569	<i>R. feae</i> (Hansen, 1921)	Guinea-Bissau	JX951315	JX951352	—	JX951402
DNA102695	AMNH LP4664	12.00250	-14.89053	<i>R. feae</i> (Hansen, 1921)	Guinea-Bissau	JX951316	JX951353	JX951376	JX951403
DNA102716	AMNH LP4663	11.88442	-14.83569	<i>R. feae</i> (Hansen, 1921)	Guinea-Bissau	JX951323	JX951360	JX951383	JX951407
DNA102720	AMNH LP4659	12.55294	-12.22761	<i>Ricinoides</i> aff. <i>feae</i>	Senegal	JX951324	JX951361	JX951384	JX951408
DNA104746	MCZ	2.74108	9.88180	<i>Ricinoides karschii</i> (Hansen & Sørensen, 1904)	Cameroon	JX951334	—	JX951393	JX951417
DNA102686	MCZ	1.25278	11.05278	<i>Ricinoides</i> cf. <i>karschii</i>	Equatorial Guinea	JX951306	JX951344	JX951370	JX951397
DNA102687	MCZ	1.25278	11.05278	<i>Ricinoides</i> cf. <i>karschii</i>	Equatorial Guinea	JX951307	JX951345	JX951371	JX951398
DNA104743	MCZ	0.50639	12.79422	<i>Ricinoides</i> cf. <i>karschii</i>	Gabon	JX951331	JX951366	—	JX951414
DNA104747	MCZ	0.50448	12.79525	<i>Ricinoides</i> cf. <i>karschii</i>	Gabon	JX951335	JX951368	JX951394	JX951418

(Continued.)

Table 1. (Continued.)

MCZ voucher	repository	latitude	longitude	ID	country	18S rRNA	28S rRNA	12S rRNA	COI
DNA105881	MRAC 230596	5.86000	-7.45000	<i>Ricinoides megahanseni</i> Legg, 1982	Ivory Coast	JX951337	—	—	—
DNA105885	MRAC 230597	5.86000	-7.45000	<i>R. megahanseni</i> Legg, 1982	Ivory Coast	JX951340	—	—	—
DNA105886	MRAC 230598	5.86000	-7.45000	<i>R. megahanseni</i> Legg, 1982	Ivory Coast	JX951341	—	—	—
DNA102682	MCZ	1.65806	10.31139	<i>Ricinoides</i> sp.	Equatorial Guinea	JX951305	JX951343	JX951369	JX951396
DNA102688	MCZ	1.31583	11.02944	<i>Ricinoides</i> sp.	Equatorial Guinea	JX951308	JX951346	—	—
DNA102689	MCZ	1.65806	10.31139	<i>Ricinoides</i> sp.	Equatorial Guinea	JX951309	JX951347	—	—
DNA102690	MCZ	1.65833	10.31556	<i>Ricinoides</i> sp.	Equatorial Guinea	JX951310-1	JX951348	JX951372	—
<i>Outgroups</i>									
Acari				<i>Ornithodoros moubata</i> (Murray, 1877)		L76355	—	NC_004357	NC_004357
Acari				<i>Haemaphysalis flava</i> Neumann, 1897		—	—	NC_005292	NC_005292
Acari				<i>Ixodes hexagonus</i> Leach, 1815		—	—	NC_002010	NC_002010
Acari				<i>Rhipicephalus sanguineus</i> (Latreille, 1806)		L76342	—	NC_002074	NC_002074
Acari				<i>Carios capensis</i> (Neumann, 1901)		—	—	NC_005291	NC_005291
Amblypygi				<i>Phrynus</i> sp.		—	—	NC_010775	NC_010775
Araneae				<i>Calisoga longitarsis</i> (Simon, 1891)		—	—	NC_010780	NC_010780
Araneae				<i>Haplopelma schmidti</i> von Wirth, 1991		AY425722.1	—	NC_005925	NC_005925
Araneae				<i>Habronattus oregonensis</i> (Peckham & Peckham, 1888)		—	—	NC_005942	NC_005942
Araneae				<i>Nephila clavata</i> L. Koch, 1878		—	—	NC_008063	NC_008063
Araneae				<i>Hypochilus thorelli</i> Marx, 1888		—	AF303505	NC_010777	NC_010777
Araneae				<i>Heptathela hangzhouensis</i> Chen, Zhang & Zhu 1981		AY425719.1	—	NC_005924	NC_005924
Scorpiones				<i>Buthus occitanus</i> (Amoreux, 1789)		—	—	NC_010765	NC_010765
Scorpiones				<i>Centruroides limpidus</i> (Karsch, 1879)		—	—	NC_006896	NC_006896
Scorpiones				<i>Mesobuthus martensii</i> (Karsch, 1879)		FJ948787.1	FJ948787.1	NC_009738	NC_009738
Scorpiones				<i>Uroctonus mordax</i> Thorell, 1876		—	—	NC_010782	NC_010782
Solifugae				<i>Eremobates palpisetulosus</i> (Fichter, 1941)		—	—	NC_010779	NC_010779
Solifugae				<i>Nothopuga</i> sp.		—	—	EU024482	EU024482
Uropygi				<i>Mastigoproctus giganteus</i> (Lucas, 1835)		AF005446	AY859587.1	NC_010430	NC_010430
Opiliones				<i>Phalangium opilio</i> Linnaeus, 1758		AF124937	—	NC_010766	NC_010766
Xiphosura				<i>Limulus polyphemus</i> (Linnaeus, 1758)		L81949	AF212167	NC_003057	NC_003057

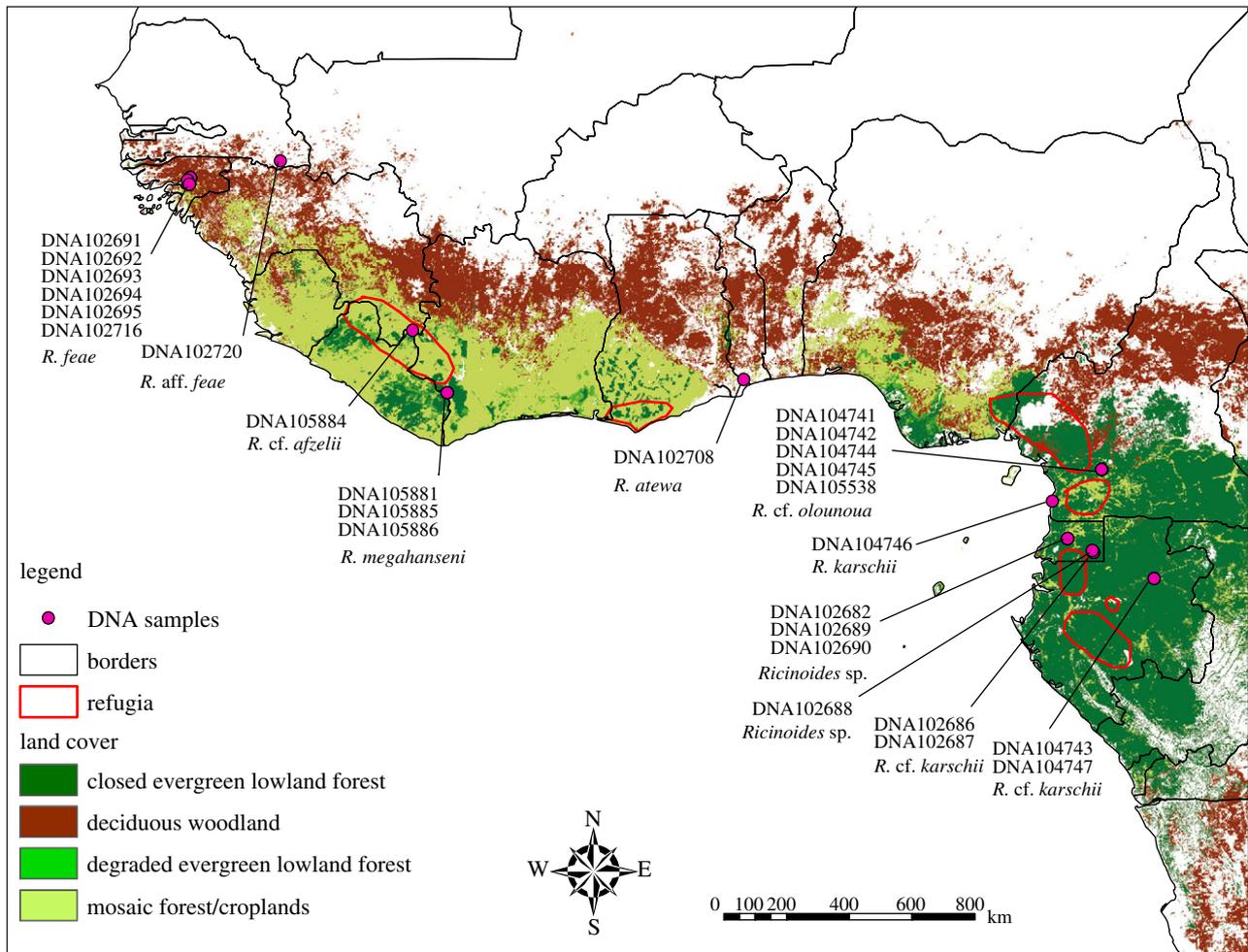


Figure 1. Map of Western and Central Africa showing localities of the African Ricinulei samples from which DNA was sequenced for the present study. Land cover map after Mayaux *et al.* [15]. Hypothetical refugia at the Last Glacial Maximum after Maley [1].

figure S1) portray climatic fluctuation as an agent of speciation and diversification.

Because of their great age [8], extreme endemism [9,10] and low vagility, Ricinulei Thorell, 1876 represent an excellent model for studying the biogeography of Western and Central Africa. Commonly known as ‘hooded tick spiders’ or ‘tick beetles’, these small (less than 11 mm) predatory arthropods are among the most obscure and cryptic of the arachnid orders [11]. A mere 72 extant ricinuleid species are currently described [12], and grouped in three genera: *Ricinoides* Ewing, 1929 from tropical Western and Central Africa, and the Neotropical *Cryptocellus* Westwood, 1874 and *Pseudocellus* Platnick, 1980. African ricinuleids are restricted to the moist soil and litter habitats of rainforests [13], whereas Neotropical ricinuleids have also been collected in caves [12].

The first molecular phylogeny of Ricinulei is presented here, with the aims of providing a temporal framework for the diversification of *Ricinoides* in Western and Central Africa, and investigating the effects of forest refugia on the generation and maintenance of tropical biodiversity.

2. Material and methods

Eleven *Ricinoides* species, recorded from 14 countries (including first record of Ricinulei from Senegal, reported here), are currently recognized in Africa [13,14]. Specimens were collected by sifting leaf litter, Winkler extraction and actively searching

in appropriate habitats (especially under logs in forested areas) throughout their known distributional range. Voucher specimens used for DNA isolation have been deposited in the following institutions: American Museum of Natural History (AMNH), New York, NY, USA; Musée Royal de l’Afrique Central (MRAC), Tervuren, Belgium; Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, MA, USA (table 1). The ingroup taxon sample comprises 26 specimens, representing at least seven ricinuleid species, from eight African countries (figure 1). Ten Neotropical ricinuleids and 20 representatives of seven other chelicerate orders were included as outgroup taxa (table 1).

DNA extraction and sequencing were conducted using protocols optimized for other arachnids [16,17] for the following genes: 12S rRNA (12S), cytochrome c oxidase subunit I, 18S rRNA (18S) and 28S rRNA (28S). Sequences were aligned using MUSCLE v. 3.7 [18]. Divergence time estimation was performed in a Bayesian framework using BEAST v. 1.5.4 [19], with an uncorrelated lognormal model of rate evolution [20]. This approach integrates the uncertainty of calibration points and topology, considered important because the phylogenetic placement of Ricinulei within Arachnida remains uncertain [21].

BEAST does not use a coupled Markov chain Monte Carlo (MCMC), potentially making it more prone to becoming trapped in local optima. A maximum-likelihood analysis was, therefore, performed using RAXML HPC v. 7.2.7 ALPHA [22] with a GTR + gamma model applied to each gene. The optimal tree was then used as an initial starting tree for BEAST. Arachnid diversification was constrained based on the oldest known fossils [23], using an exponential distribution prior and setting the standard deviation to obtain a 95 per cent range between 428 (oldest

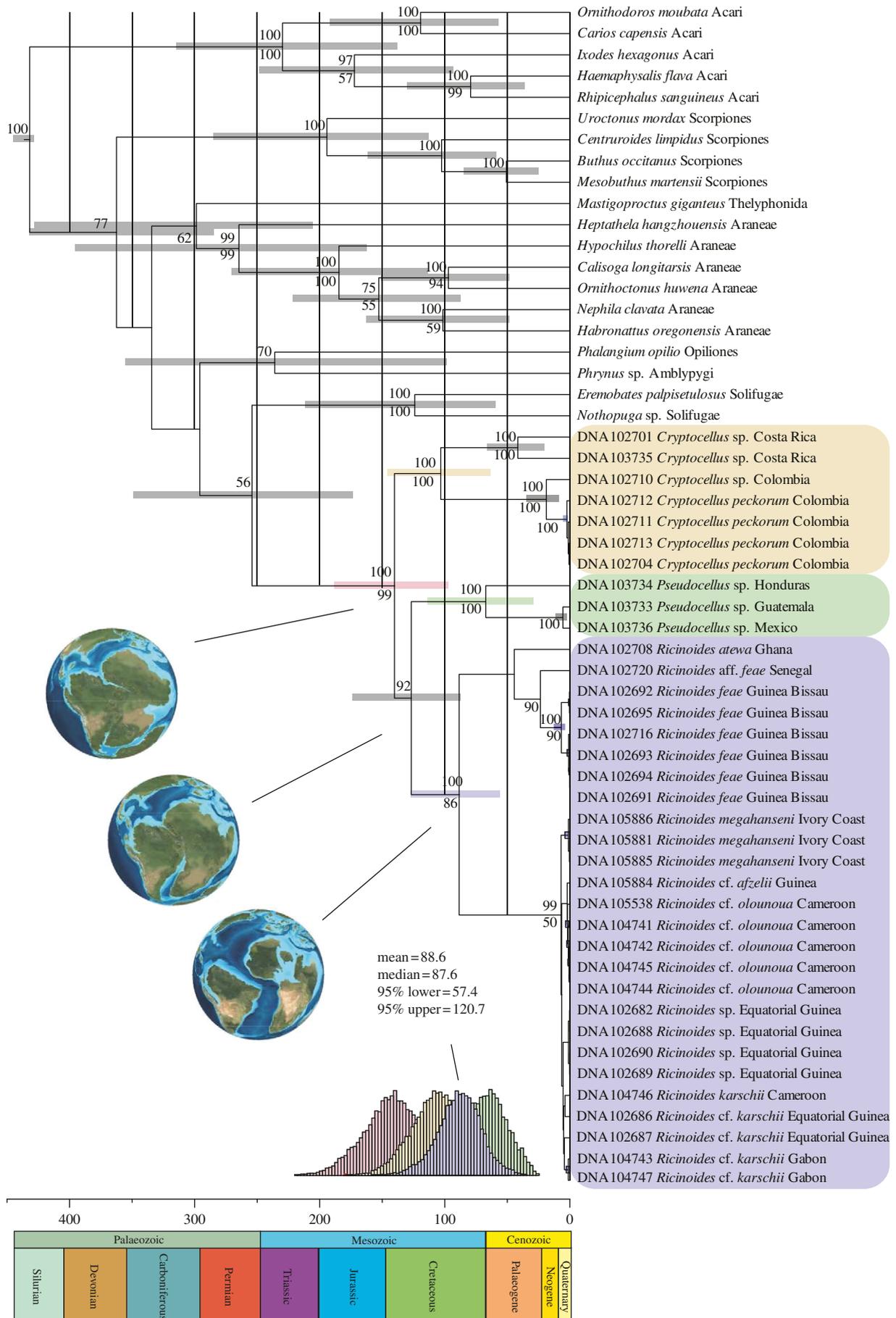


Figure 2. Maximum credibility tree for African Ricinulei and outgroup taxa, obtained by Bayesian inference in BEAST [19]. 95% Confidence intervals for ages are represented by bars at nodes. Clade posterior probabilities above 50% are indicated above nodes and maximum-likelihood bootstrap frequencies below nodes. Posterior distributions for nodes of interest are also depicted below the tree. Palaeogeographic maps from Ron Blakey, NAU Geology at <http://jan.ucc.nau.edu/~rcb7/>.

known fossil arachnid, a scorpion) and 445 Ma (oldest known fossil chelicerate, a horse-shoe crab). The BEAST analysis was run for 60 million generations with sampling every 1000 generations.

3. Results and discussion

The results recover the monophyly of Ricinulei and its component genera, *Cryptocellus*, *Pseudocellus* and *Ricinoides*, with high support (figure 2). The origin of the group (the divergence from its sister group) is dated to around 250 Ma. The oldest known fossil ricinuleid (not considered part of the Neoricinulei crown group), dated to 319 Ma [24], is concordant with the 95% confidence interval on the tree, and independently corroborates the analytical results and biogeographic conclusions. *Ricinoides* is sister to one of the two Neotropical genera, *Pseudocellus*, suggesting that the entire diversification of Ricinulei predates the fragmentation of Gondwana. This biogeographic interpretation, previously proposed based on morphological evidence [25], is corroborated by the molecular dating. Based on the results presented here, the diversification of *Ricinoides* in Western and Central Africa occurred in the Late Cretaceous, around 88 ± 33 Ma. Specimens from Guinea and Ivory Coast group with those from Cameroon, Equatorial Guinea and Gabon, probably an artefact of missing data (lack of mitochondrial gene sequences for the former; table 1). Samples from the Ivory Coast group with the remaining West African samples in the maximum-likelihood analysis, as expected based on their similar morphology and geographical proximity. Among the West African samples, the divergence between *Ricinoides atewa* Naskrecki, 2008 and other species from Senegal and Guinea-Bissau is dated to around 44 Ma.

Tropical forest biodiversity is lower in Africa than in South America and Southeast Asia [26]. This difference has been attributed to extinctions caused by forest fragmentation and potentially even the complete disappearance of the forest during past periods of severe aridification [5]. This is exemplified by the low diversity of another ancient group of soil animals, velvet worms (*Onychophora* Grube, 1853), with a single species of Peripatidae Evans, 1901 in tropical Africa (Gabon and Cameroon), when compared with four species in Southeast Asia and 68 in the Neotropics [27]. The relatively low diversity of the tropical African forests is consistent with the majority of molecular evidence, which suggests that rainforest endemics are mostly recent (Late Miocene–Pleistocene) and diversified according to the refugial speciation model [4].

The results presented provide molecular evidence for an endemic African rainforest taxon, *Ricinoides*, the origin of which can be traced to the fragmentation of Gondwana,

and confirms evidence from other ground-dwelling arthropods [28] for an early diversification in the Late Cretaceous, around 90 Ma, in Western and Central Africa. This period corresponds to a time of diversification among angiosperms and associated reduction in gymnosperm diversity, documented in the Cenomanian stage of the Late Cretaceous [29]. Even if the Mesozoic rainforests were structurally and compositionally different from those in present-day tropical Africa, stratified forests may have been present since the Late Cretaceous, based on the presence of large seeds and fruits in the fossil record [30]. The major divergence observed among species in Western and Central Africa around 90 Ma could be the result of vicariance caused by successive marine incursions (figure 2) that commenced in the Late Cretaceous [31]. Refugia may also have played a role in allopatric speciation on a smaller scale for more recent species in the area of present-day Cameroon and Gabon.

The results presented suggest further that ancient diversifications exist in Western and Central Africa and the biodiversity of this region may have been greater during Late Cretaceous to Palaeocene times. Climate change may have depleted diversity after the separation of Africa and South America, with subsequent stable refugia acting as ‘museums’ for ancient lineages. In this respect, the data are largely congruent with the fossil record, which suggests that entire lineages of Neotropical palms were present in Africa until at least the Late Oligocene (27–28 Ma) [7]. Such models [5] may have received little support from molecular studies until now (but see [6]), because few phylogeographic studies have been conducted on old lineages with high endemism and low population density (see electronic supplementary material). Furthermore, extinction rates are difficult to infer from molecular studies [32] in the absence of fossils from outside the putative refugia. *Ricinoides* thus represents one of the oldest endemic African genera for which the origin, early diversification and subsequent survival in Miocene forest refugia has been studied and tested phylogenetically.

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