A living fossil tale of Pangaean biogeography

Jerome Murienne[1,2], Savel R. Daniels[1,3], Thomas R. Buckley[4,5,6], Georg Mayer[7] and Gonzalo Giribet[1]

[1]Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA
[2]CNRS, Université Paul Sabatier, ENFA, UMR 5174 EDB (Laboratoire Évolution et Diversité Biologique), Université de Toulouse, 118 route de Narbonne, Toulouse 31062, France
[3]Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa
[4]Landcare Research, Auckland Mail Centre, Private Bag 92170, Auckland 1142, New Zealand
[5]School of Biological Sciences, University of Auckland, Auckland, New Zealand
[6]Allan Wilson Centre for Molecular Ecology and Evolution, Auckland, New Zealand
[7]Animal Evolution and Development, Institute of Biology, University of Leipzig, Talstraße 33, Leipzig 04103, Germany

The current distributions of widespread groups of terrestrial animals and plants are supposedly the result of a mixture of either vicariance owing to continental split or more recent trans-oceanic dispersal. For organisms exhibiting a vicariant biogeographic pattern—achieving their current distribution by riding on the plates of former supercontinents—this view is largely inspired by the belief that Pangaea lacked geographical or ecological barriers, or that extinctions and dispersal would have erased any biogeographic signal since the early Mesozoic. We here present a time-calibrated molecular phylogeny of Onychophora (velvet worms), an ancient and exclusively terrestrial panarthropod group distributed throughout former Pangaean landmasses. Our data not only demonstrate that trans-oceanic dispersal does not need be invoked to explain contemporary distributions, but also reveal that the early diversification of the group pre-dates the break-up of Pangaea, maintaining regionalization even in landmasses that have remained contiguous throughout the history of the group. These results corroborate a growing body of evidence from palaeontology, palaeogeography and palaeoclimatic modelling depicting ancient biogeographic regionalization over the continuous landmass of Pangaea.

1. Introduction

Following the validation of the plate tectonics in the 1960s, the idea that the contemporary distribution of species on a global scale was related to continental split became widely accepted in the biogeographic literature. However, the generalized use of molecular phylogenetics and divergence time estimations have challenged this notion, demonstrating that some biotas were considerably younger than previously thought and that trans-oceanic dispersal was more widespread than hitherto postulated [1–5]. The recent biogeographic literature has swarmed with examples refuting the role of continental split in shaping the current patterns of species distribution, but this might simply be a result of the following factors. As recently noted by Beaulieu *et al.* [6], most biogeographic studies addressing the question of continental vicariance are based on low-level taxonomic groups (such as genera or families) exhibiting a particular disjunction pattern. In those cases, the inferred dispersal scenario is simply a consequence of the group not being old enough to be influenced by tectonic movement in the first place. In fact, a few examples of global distributions rooted to the continental break-up still exist, with prominent cases in old lineages of animals [7–9] and plants [6,10]. Another issue emerges from the previous statement: in many old groups that could be good models for historical biogeography, vagility often blurs the biogeographic signal and inferring historical scenarios might simply be impossible. Plainly, the older a group is, the more likely it is that
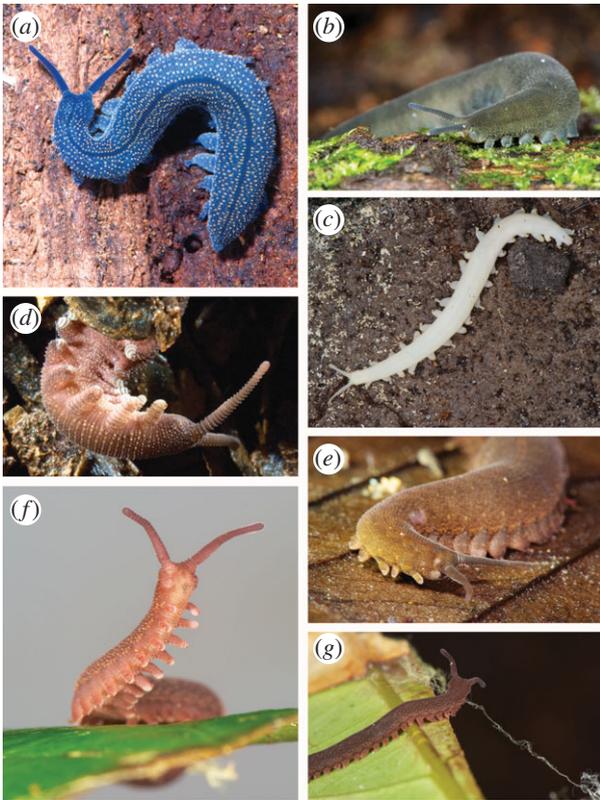
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Figure 1. Live images of selected species of Onychophora showing habitus and behaviour. (*a*) *Peripatoides aurorbis* from Kahurangi National Park, New Zealand (Peripatopsidae). (*b*) *Peripatopsis moseleyi* from Karkloof Nature Reserve, South Africa (Peripatopsidae). (*c*) *Peripatopsis alba*, an endangered cavernicolous species from the Wynberg cave system in Table Mountain, South Africa (Peripatopsidae). (*d*) *Mesoperipatus tholloni* from the Ogooue river basin, Gabon (Peripatidae). (*e*) *Macroperipatus* sp. from Reserva Ducke, Amazonas, Brazil (Peripatidae). (*f*) An unidentified Peripatidae from the Rio Negro, Roraima, Brazil. (*g*) Same specimen as in (*f*) delivering its glue threads. (Online version in colour.)

the distributions of the species have changed over time, confounding inference of ancestral areas [6].

We here present a time-calibrated global molecular phylogeny of Onychophora (velvet worms), the only animal phylum nowadays confined to terrestrial habitats throughout their life (figure 1*a*−*g*). Despite the low number of described species (less than 200 worldwide), they constitute an ideal model system for biogeographic analyses [11]. The group presents a wide distribution classically interpreted in the framework of continental break-up, but the species are typically considered narrow endemics. They currently live in moist temperate to tropical forests and we include specimens from most major landmasses (New Zealand, Tasmania, Australia, South Africa, southern South America, the Neotropics, Caribbean, equatorial Africa and Southeast Asia). Their early diversification has recently been estimated using multiple phylogenomic datasets [12] and found to be associated with the appearance of the first forests in the Devonian *ca* 382 Ma [13]. Onychophorans are also important from a biogeographic point of view owing to their low vagility, high susceptibility to desiccation and their fastidious habitat requirements [11,14]. Along these lines, experimental work has shown that velvet worms are slow-moving animals that avoid daylight and weak wind currents—both being main causes of desiccation—and the animals died after 14–18 min floating in seawater [15]. This also correlates with

their short-range endemism [16], deep genetic population structure [17] as well as small population sizes susceptible to high ecological impact [18]. These characteristics, along with their antiquity, render velvet worms an unparalleled model to study ancient biogeographic events.

The sequence of continental splits allows us to formulate specific predictions about the expected phylogenetic relationships and timing of cladogenesis (see [19] for an example on Southern Hemisphere biogeography). In order to test whether the current distribution of velvet worms and their diversification were reached through ancient vicariant events [11,20], we investigated the phylogenetic and biogeographic history of the group by sampling their major distribution centres, including samples from nearly all major landmasses they inhabit. We reconstruct the evolutionary history of the group using molecular phylogenetics and apply various dating techniques using multiple calibration points. The timeframe of the cladogenetic events are then compared with recent global plate motion reconstructions [21], and discussed in the framework of Pangaean palaeogeography and palaeoclimate.

2. Material and methods

(a) Material, DNA isolation and sequencing
Specimens were collected in all major landmasses where onychophorans occur, except India and New Guinea. These include 15 samples of Peripatidae from Malaysia, Gabon, the Greater Antilles, Mesoamerica and northern South America, including the major generic diversity of the family, and 46 specimens of Peripatopsidae from Chile, South Africa, Australia, Tasmania and New Zealand (see electronic supplementary material, table S1). All voucher specimens and genetic materials have been deposited in the Museum of Comparative Zoology (Harvard University, Cambridge, MA).

For this study, we used the mitochondrial protein-encoding gene *cytochrome* c *oxidase subunit I* (*COI* hereafter), the mitochondrial genes *12S rRNA* and *16S rRNA*, and fragments of the nuclear ribosomal genes *18S rRNA* and *28S rRNA*. All new sequences have been deposited in GenBank (see electronic supplementary material, table S1).

(b) Calibrations
The root of the tree was calibrated based on the date estimates obtained in a broader context. Rota-Stabelli *et al.* [12] used a comprehensive dataset of extant Ecdysozoa (panarthropods and related taxa) calibrated with a set of 30 relevant points across recently published phylogenetic datasets. They consistently estimated the diversification of Onychophora to be associated with the appearance of the first forests in the Devonian *ca* 382 Ma [13]. In order to be conservative, we chose to use the youngest of those estimates—which have the lowest potential to reject the hypotheses of oceanic dispersal. In order to incorporate the uncertainty in the calibration (corresponding to the error margin in the date estimates of [12]), we modelled the prior information using a normal distribution centred at 382 Ma with a standard deviation of 25 Myr. Even though Palaeozoic onychophoran fossils have been reported from Mazon Creek, USA [22] and Montceau-les-Mines, France [23,24], they could not clearly be attributed to one of the extant families and were not used in this study. However, we used the oldest unambiguous extant onychophoran fossil, found in the Myanmar (Burmese) amber, which belongs to Peripatidae [25] (see the electronic supplementary material for details on the fossil). For this calibration, we used a lognormal distribution with an offset of 100 Myr and

set the standard deviation so that 95% of the distribution would be younger than the age of the root.

(c) Divergence times

In order to be able to integrate the topological and fossil uncertainty, divergence time estimation was performed in a Bayesian framework using BEAST v. 1.7.5 [26] while testing different dating models (see the electronic supplementary material).

3. Results

(a) Onychophoran phylogenetics

This is the first study addressing the global phylogeny of Onychophora including samples from virtually all landmasses. A few previous studies have focused on subsets of Peripatopsidae [11,27] or Peripatidae [28,29], but these are more restricted in geographical and taxonomic scope. Our tree with outgroups (see the electronic supplementary material, figure S1) clearly shows a split between the two major clades: Peripatidae, of tropical distribution, and Peripatopsidae, found on the southern landmasses that once surrounded Antarctica in temperate Gondwana (figures 2 and 3). Within Peripatidae, the first split separates the Southeast Asian *Eoperipatus* from the western Gondwanan clade (figure 2), as shown in a recent study including the first sequence data on *Eoperipatus* [28]. The monotypic *Mesoperipatus* from Gabon appears as the sister group of a monophyletic Neotropical clade, which divides into an Andean and a mostly Caribbean/Mesoamerican clade that shows little correspondence to the current generic divisions of Peripatidae. Sampling within Peripatidae is limited, however, as it is missing much of the recently discovered Amazonian and Brazilian diversity [29,30].

Peripatopsidae is densely sampled and shows biogeographic signal (figure 2) associated with Southern Hemisphere continental fragmentation. The Chilean *Metaperipatus* appears nested within the South African species, as the sister group to *Peripatopsis*, with *Opisthopatus* branching prior to this 'trans-oceanic' divergence [11,16]. The continental Australian faunas segregate into the wet Western Australian forests and the Eastern Australian region, which forms a continuous belt of diversity from New South Wales to the Wet Tropics. The third clade shows two instances of Tasmania/New Zealand vicariance [31]: one for *Ooperipatellus*, and another including a few Tasmanian species and the New Zealand endemic genus *Peripatoides*.

The only minor difference between the Bayesian maximum clade credibility tree depicted in figure 2 and the ML tree obtained with RAxML (see the electronic supplementary material, figure S2) is that the Australian group (Western + Eastern regions) is monophyletic with 72% posterior probability in the Bayesian tree but paraphyletic with respect to the Tasmania/New Zealand in the ML tree.

(b) Divergence times

We report the results obtained with a Yule speciation prior and an uncorrelated lognormal distribution (UCLD) dating model (figure 2) as it was found to be the top-ranking combination using thermodynamic integration (path sampling). While there was no significant difference between a Yule and a birth–death speciation prior, the UCLD model was found to be significantly better than the other models (logBF > 5). As opposed to strict clock or autocorrelated models, the UCLD model does not require rates to be heritable from parent node to child node through the phylogeny. We used two additional metrics to evaluate the appropriateness of the UCLD model. The covariance statistic spans zero with 95% highest probability density comprised between −0.1568 and 0.2013, suggesting that there is no strong evidence of autocorrelation of rates in the phylogeny. We also examined the coefficient of variation (median: 0.32, 95% HPD: 0.2408–0.4163), suggesting that rates vary more than 30% from the mean.

Results from the sensitivity analysis are also depicted in figure 2. We show the median estimates of the dates obtained under alternative Bayesian methodologies, while ML estimates (penalized likelihood) represent optimal dates. Our results suggest that younger estimates always fall within the credibility interval of the UCLD model while older estimates can be much older, especially for Peripatopsidae. This also suggests that the optimal results obtained under the UCLD model are conservative.

Divergence time estimates show that no oceanic dispersal is required to explain the current distribution of the exclusively terrestrial velvet worms. This applies especially to all major divergences between continents. For the New Zealand/Tasmania divergences (two instances), our estimates overlap with the initiation of seafloor spreading between New Zealand and Australia [32] (figure 4). However, there is considerable uncertainty as to when exactly land connections to the north of New Zealand were finally disrupted [34]. In any case, our estimates (median: 77.7, 95% HPD: 55.4–103.0; median: 75.1, 95% HPD: 53.4–100.7) are also older than the supposed Oligocene drowning episode (ca 22 Ma [35]). Major cladogenetic events within Peripatopsidae are ancient, such as the split of *Metaperipatus* from Chile and *Peripatopsis* from South Africa (median: 141.3, 95% HPD: 101.4–184.6) or the continental Australia versus (Tasmania + New Zealand) divergence (median: 121.7, 95% HPD: 89.4–159.0). The youngest divergence between the Antilles and the continental species dates back to the Cretaceous/Palaeogene (median: 62.4, 95% HPD: 42.5–88.4), much more recent than the formation of the Caribbean region during Pangaean break-up in the Jurassic. This supports the hypothesis of the Proto-Antilles in the Late Cretaceous and the connection between the Antilles and South America until the Mid-Cenozoic [36]. However, much denser taxon sampling will be required to test the complicated geological history of the Caribbean region [37].

The early cladogenetic events within each family precede the break-up of Gondwana (figure 3), even when considering the uncertainty of the event [21,32,38–41]. The split between Equatorial Africa and the Neotropics may be Triassic (median: 242.9, 95% HPD: 321.8–174.9) and their diversification from *Eoperipatus* Permian (median: 285.6, 95% HPD: 211.7–369.6), whereas the split within the temperate Gondwanan species may be Jurassic (median: 181.4, 95% HPD: 232.5–134.6).

4. Discussion

(a) Biogeographic patterns

The sequence of continental splits allows for the formulation of specific predictions regarding the evolutionary relationships, biogeographic pattern and timing of cladogenesis that can be tested using a molecular framework. Despite their recent predominantly Gondwanan distribution, our
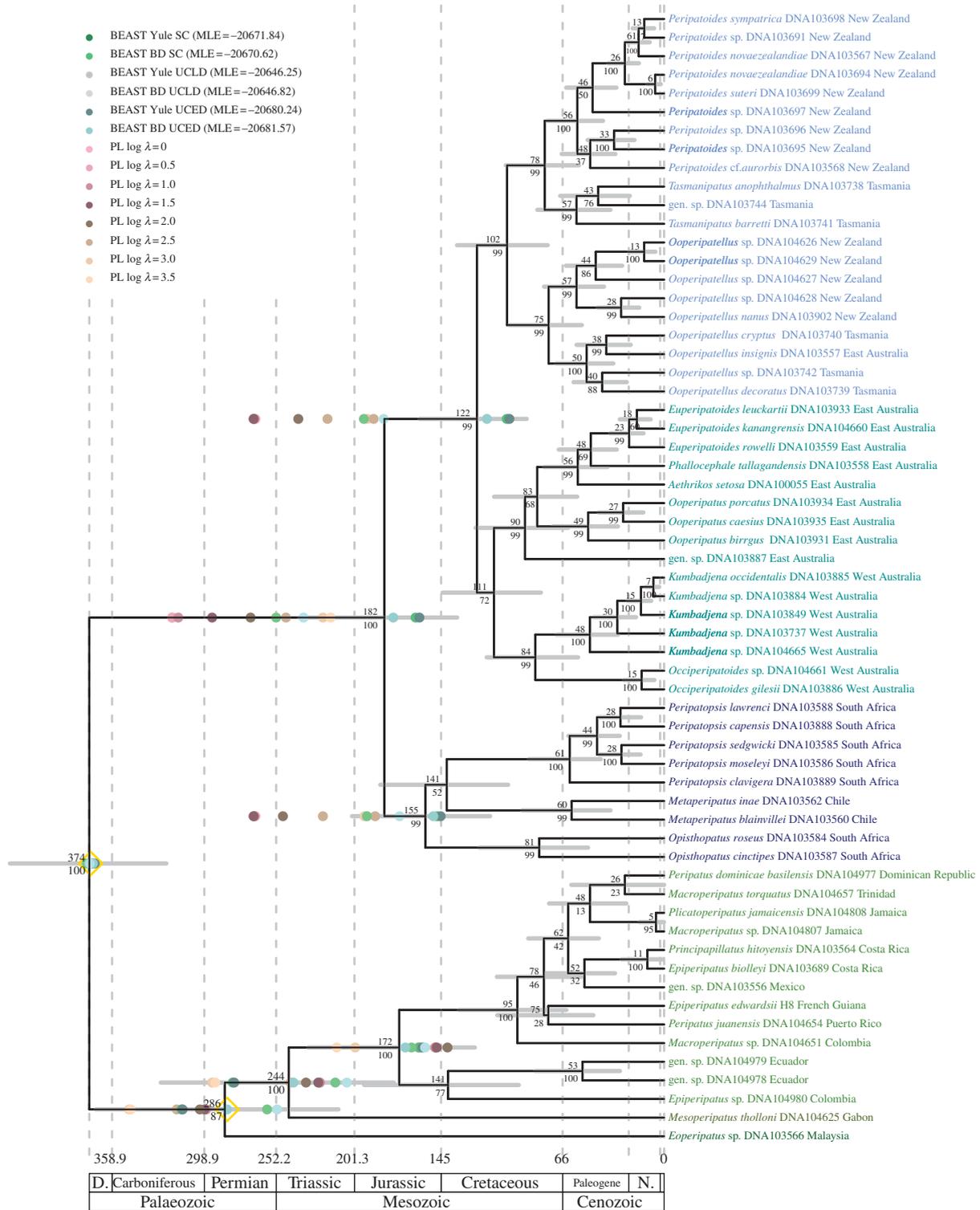
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Figure 2. Chronogram of the sampled specimens with members of Peripatidae (tones of green) and Peripatopsidae (tones of blue) inferred under an uncorrelated lognormal (UCLD) model with a Yule speciation prior. Numbers at nodes indicate clade posterior probabilities; grey bars indicate 95% highest probability density. Gold diamonds indicate calibrated nodes. Points indicate date estimates (median for Bayesian and optimal of ML) obtained under alternative dating models. BD, birth–death; SC, strict clock; UCED, uncorrelated exponential; PL, penalized likelihood. 2012 Stratigraphic chart according to the International Commission on Stratigraphy.

divergence time estimations suggest that onychophorans were distributed throughout the ancient supercontinent of Pangaea. The latter observation is corroborated by fossil data, as specimens probably belonging to Peripatidae have been found in Baltic and Dominican ambers [25,42,43]. In addition, the more ancient Carboniferous fossils from the deposits of Mazon Creek [22] (IL, USA) and Montceau-les-Mines [44] (France) were located in the northern part of Pangaea. We found that the split between the Southeast Asian peripatid species and the remaining Peripatidae can be dated back to the Late Palaeozoic, at a time when velvet worms could have achieved a broad distribution across Pangaea. Subsequent climate changes in the Northern Hemisphere, particularly in Europe and North America, may have led to the extinction of the fauna in these regions as the climate became progressively colder.
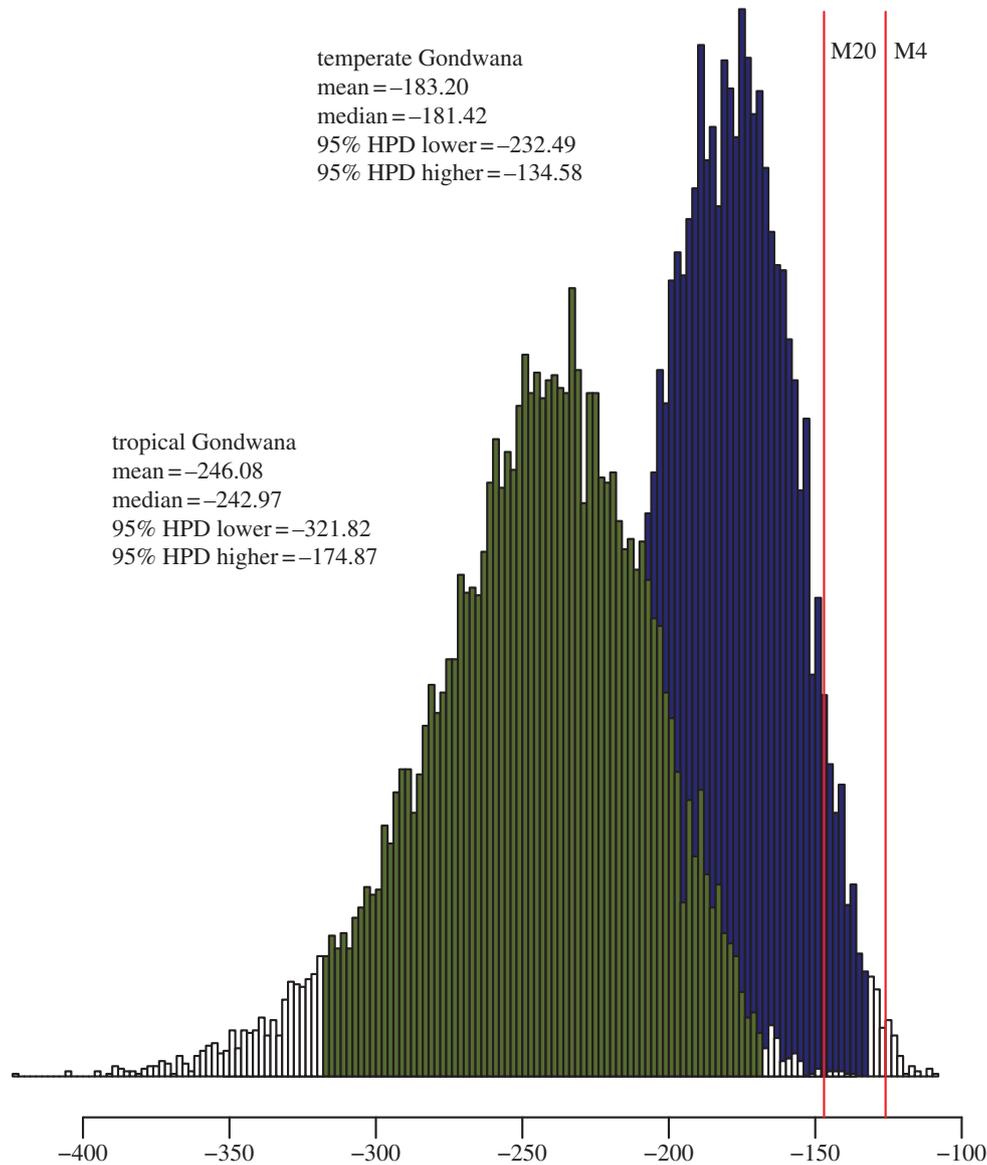
Figure 3. Posterior probability densities obtained under the optimal uncorrelated lognormal (UCLD) model with a Yule speciation prior for the Equatorial/Neotropical split (green) and the temperate Gondwanan group (blue). Ages of the corresponding oldest unambiguous magnetic anomalies are indicated in red (see figure 4; electronic supplementary material). (Online version in colour.)

Within Peripatidae, a clear phylogenetic link between the Neotropical and West African species occurred until the Triassic. This age clearly refutes the possibility of a trans-oceanic dispersal and indicates a possible cladogenetic event pre-dating the separation of Africa from America. Interestingly, a similar conclusion has been found recently in two studies of soil-dwelling arachnids [8,45]. In the harvestman group Cyphophthalmi, the split between the Equatorial African family Ogoveidae and the family Neogoveidae, the latter found both in the Afrotropics and the Neotropics, has been dated to ca 261 Ma [8]. In the same fashion, the early diversification of the arachnid order Ricinulei, confined to the tropical forests of the Neotropics and Equatorial Africa, is dated to ca 250 Ma [45]. Both of these dates are similar to our estimates for velvet worms in that they pre-date the break-up of Gondwana, even when considering plate models that extend over at least a few hundred million years and treat plates as dynamic features with dynamically evolving plate boundaries [21,38–41] (see a discussion of Gondwanan break-up in the electronic supplementary material). Within the temperate Gondwanan Peripatopsidae, the earliest divergence between eastern (Australasia) and western Gondwana (Chile–South

Africa) occurred during the Jurassic ca 182 Ma, largely pre-dating the opening of the Drake Passage between America and Antarctica at 41 Ma [46].

Under a classical scenario of vicariance owing to the separation of continents, we would expect to find reciprocal monophyly of each group carried by each continent. Surprising results are those of Chile–South Africa and New Zealand–Tasmania, as neither the faunas from South Africa nor New Zealand and Tasmania are monophyletic. Interestingly, South African *Peripatopsis* and Chilean *Metaperipatus* share two features that are not found in other onychophorans: (i) dermal insemination and (ii) trophic embryonic vesicles [47,48], putative synapomorphies for this clade. A paraphyletic assemblage in a region could be explained by more recent trans-oceanic events, but the life-history characteristics of Onychophora, together with our divergence time estimates, clearly refute this scenario. Our results indicate that for those regions, the groups had most probably diversified prior to the separation of the continental landmasses, and this ancestral cladogenesis could reflect the rifting process preceding the continental break-up [49]. Similar non-monophyletic assemblages of faunas in New Zealand and South Africa have also been
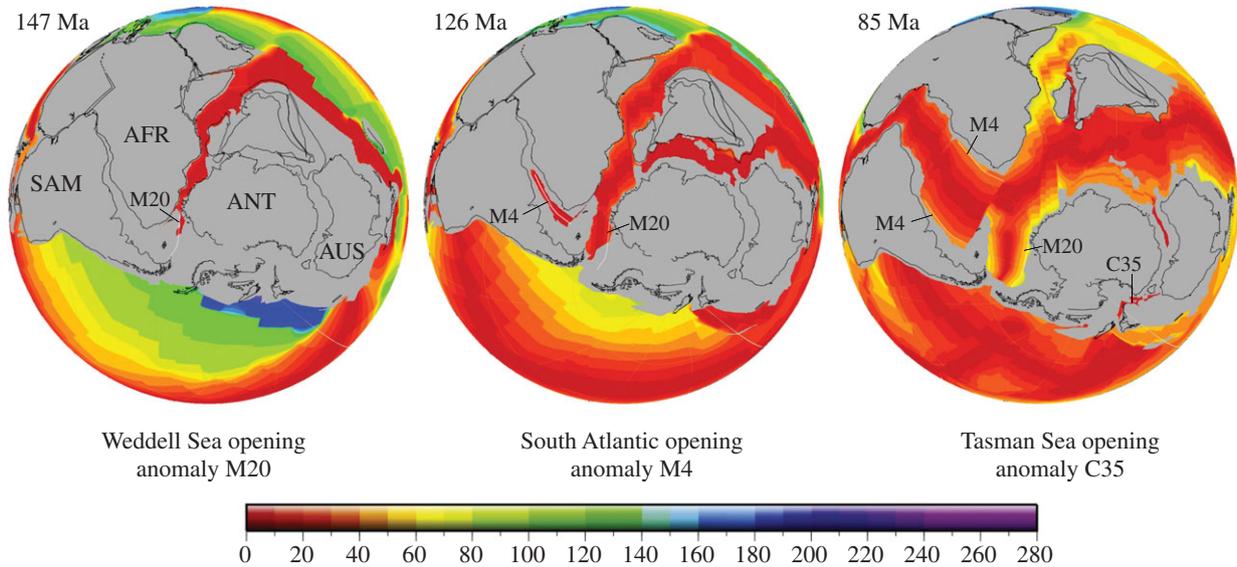
Figure 4. Palaeogeographic reconstructions according to Seton *et al.* [21] and Müller *et al.* [33] showing the ages of the relevant magnetic anomaly isochrons associated with seafloor spreading. Colour bar indicates the age of oceanic lithosphere. Current coastlines are depicted in black and isochrons in white. SAM, South America; AFR, Africa; ANT, Antarctica; AUS, Australia. (Online version in colour.)

observed in other ancient ground-dwelling animals, such as earthworms [50], the harvestman family Pettalidae [51] and the centipede genus *Paralamyctes* [52]. However, other classical models of Gondwanan vicariance, including cichlid fishes, have been recently refuted [53].

(b) Ancestral provincialism

By studying one of the oldest terrestrial groups, with strikingly limited dispersal abilities, we were able to demonstrate that no oceanic dispersal is required to explain the current distribution of the group, as in recent reports on terrestrial leaf-litter arthropods [8,9,45,52]. A key contribution of this study is to show that the early diversification of velvet worms actually pre-dates continental split (figure 3), a result that resonates with recent molecular phylogenetic studies showing that cladogenesis in the major lineages of Cupressaceae (a gymnosperm family) [10] and amphibians [54] also pre-dated the break-up of Pangaea. Under this scenario, the fragmentation of landmasses would have only dragged, along rifting continents, lineages that were already separated.

While finding a model organism that is able to retain biogeographic signal over such a time scale might be extremely difficult, those results are not unexpected. Continental break-up and its preceding rifting are not the only mechanisms leading to vicariance, as physical or environmental barriers can also lead to speciation processes over contiguous landscapes. Indeed, many of the classical examples of vicariance put forward by Ernst Mayr in the 1940s to support the theory of geographical speciation involved contiguous land. In a similar fashion, the refuge theory developed in the 1960s envisioned a mechanism where Amazonian species became isolated in small patches of rainforest during arid periods of the Pleistocene, ultimately leading to allopatric speciation [55]. With the rise of molecular phylogenetics and divergence time estimation, there are now a plethora of examples depicting speciation processes over contiguous land. Barriers could be geographical (such as rivers [56], marine incursions [45] or rifting [49]) or ecological (most notably involving contraction of habitat in relation to past climatic changes [57]). In such a

context, several factors could have led to the formation of barriers over Pangaea. As noted by Scotese [58], there were important barriers to migration of terrestrial organisms over Pangaea, most notably mountain ranges. In addition, geological studies as well as palaeoclimatic modelling have long depicted strong provincialism in temperature and precipitation over some regions of Pangaea [59–62]. This regionalization was not static and has been affected by various cycles of glaciation during the Late Palaeozoic Ice Age [63,64], in turn affecting floristic dynamics [65]. The Late Palaeozoic deglaciation (from *ca* 300 Ma to *ca* 260 Ma) induced substantial changes over Pangaea [66–68]. Those include the expansion of deserts and the contraction of forests, as depicted by climate–biome models [69,70]. This had a strong influence on species distributions, with an increase in diversity of the flora in the Northern Hemisphere and Gondwana [71], and a decline and turnover for the palaeotropical wetland forests [72–74]. This rainforest collapse has been shown to drive rapid diversification of tetrapods in Euramerica [75]. The Permo-Triassic mass extinction had a profound and drastic impact on most forms of life on the planet, with an estimated 70% extinction of terrestrial animals. This resulted in a global ecological release that drove species diversification and increased provincialism [76]. In addition, strong biotic provinciality was also related to cyclical climatic modes during the early Mesozoic [77].

It is now well established that many of the terrestrial groups (including plants, insects, myriapods, arachnids, velvet worms and nematodes) diversified during the Palaeozoic [12,78]. The extensive regionalization and dynamic nature of Pangaean environments (in terms of both habitats and climate) provide a simple and obvious framework for interpreting these diversifications. However, velvet worms might be one of only a few groups that were able to retain a strong biogeographic signature of speciation events over such a long time frame.

(c) Final conclusions

By amassing exemplars from virtually all the landmasses where velvet worms occur today, and by applying sophisticated methods of data analysis and diversification time

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estimates, we show that an ancient terrestrial group, with nearly global distribution, has diversified prior to major tectonic events. As in many other ancient groups [9], velvet worm faunas may have gone extinct on entire terranes (e.g. Antarctica), probably owing to past environmental change, but despite the signal erased by extinction, these animals still constitute a key example to understand vicariance biogeography and ancestral cladogenesis.

On a more recent time scale, our results call for a re-examination of Gondwanan biogeography. The congruent patterns of diversification among various groups of invertebrates, including velvet worms, earthworms, harvestmen, ricinuleids and centipedes, to mention just a few recently characterized examples, might shed light on ancient palaeogeographic or palaeoenvironmental barriers pre-dating the fragmentation of Gondwana. Such barriers might have existed between the northern Neotropical/Palaeotropical region (tropical western Gondwana) and the southern Chile/South Africa region (temperate western Gondwana), as well as along the tropical Australia versus temperate Australia/New Zealand region. Interestingly, in many soil animals with low vagility, as is the case of velvet worms, few faunal components are shared between these tropical and temperate regions, despite the persistence of contiguous landmasses throughout Earth's history [8,79].

Historical biogeography in general needs to refocus on analysing groups of organisms that are not only old enough to be able to track continental break-up episodes, but also have limited dispersal abilities in order to avoid erasing the biogeographic signal. Finally, our study also calls for careful use of continental break-up age for calibration as those events could also represent minimum constraints on diversifications.

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