CellPress

Relict species: a relict concept?

Philippe Grandcolas[1], Romain Nattier[1], and Steve Trewick[2]

[1] Institut de Systématique, Evolution, Biodiversité (ISYEB), UMR 7205 CNRS MNHN UPMC EPHE, Muséum National d'Histoire Naturelle, CP 50, 75005 Paris, France
[2] Ecology Group, IAE, Massey University, Private Bag 11-222, Palmerston North, New Zealand

Relict species have always beguiled evolutionary biologists and biogeographers, who often view them as fascinating 'living fossils' or remnants of old times. Consequently, they are believed to provide interesting and important information on a vanished past and are used to understand the evolution of clades and biotas. The information that relicts provide can, however, be misleading and overemphasised when it is not remembered that they belong to groups or biotas that are mostly extinct. For example, relict species imply regional extinctions and, for this reason, they cannot simultaneously provide evidence of local biota permanence. Here we consider carefully misconceptions about relict species and highlight more clearly their evolutionary and biogeographical significance.

Relicts and sampling in evolutionary and biogeographical studies

Interpreting the evolutionary history of species and biotas is heavily dependent on sampling extant taxa. By tradition, evolutionary studies begin by identifying the characteristics of taxa and the geographical distribution of the various taxon groups that are present. Phylogenetic tools contribute by providing both a hypothesis of relationships and a timescale for diversification. However, whether pursued via *ad hoc* reasoning or formalised analyses (e.g., character analysis, molecular phylogenetics and dating, area clade analysis), the primary data are sampled taxa. The distribution of characters or geographical distributions – the main features of interest to evolutionary biologists – is uneven in lineages through time in the fossil record, and all phylogenetic analyses are sensitive to this [1,2]. An extreme expression of the sampling problem is that of so-called 'relict' species. These organisms are often viewed as providing compelling evidence for conservation of ancestral character states in terms of morphology, ecology (e.g., [3–5]), and spatial distribution (e.g., [6–8]). However, given their relict status, they belong to groups that are mostly extinct and as such, by definition, provide deficient samples (Box 1). This can be especially misleading when relicts are considered as key to the interpretation of exceptional evolutionary cases, by traditionally assuming that they indicate evolutionary stasis, or the permanence of biota, in either continental islands or diversity

centres [9–11]. Their evolutionary and biogeographical significance therefore needs to be revisited.

Relicts do not imply conservation of characters

Before the rise of modern phylogenetics, evolutionary reasoning by intuition focussed on notions of grades and evolutionary intermediates and on species comparisons considered in the framework of ancestor–descendant relationships, even at a macroevolutionary scale. Modern phylogenetic approaches changed the way of thinking by showing that an ancestor cannot be identified with certainty; it would be expected to have all characters in an ancestral state relative to other species hypothetically taken as descendants. This situation never occurs because every species evolves, even if only at a few characters [9,12–15]. Consequently, phylogenetic relationships involve sister-group relationships and taxa are taken as mosaics of ancestral and derived character states. In this modern and generally acknowledged context, relicts are

Glossary

Basal species: a widely used but incorrect term, poorly descriptive of the topology of a phylogenetic tree, suggesting that a small group is closer to the root than its larger sister group and, therefore, shares more features with the ancestor. Instead of basal, a species should be termed as a 'sister group of the remainder' [15,17,19]. Basal refers to the relative placement of the node from which the lineage arises but says nothing about the characters expressed by the extant species at the lineage tip. The relevant lineage is better described as 'early branching', or arising from deepest node in the clade of interest.
Living ancestor: the logic of phylogenetic inference demonstrates that an ancestor cannot be identified because it should be for all characters in an ancestral state compared with related taxa; otherwise, it would be nested within a group and not be ancestral [13]. This renders 'living ancestor' a term that suggests an impossible inference.
Living fossil: referring to a relict, by emphasis on the unbalanced ratio between extinct and living species within the clade under study. This is an oxymoron linked to terms such as living ancestor, implying that living taxa express fossilised characters.
Missing link: used to qualify a taxon that is supposed to show a combination of characters explaining an evolutionary transition when such a need cannot be substantiated *a priori* (transitions can be abrupt or punctuated). Such a taxon is often sought in the fossil record or among relict species. The concept of the missing link or evolutionary intermediacy was also misleadingly embodied into the criterion for homology by connection by intermediates.
Panchronic species: used to emphasise apparent evolutionary stasis, with some extant species that did not change from a particular point of view (most often morphological), over protracted evolutionary time. This misleadingly entails that species are not mosaics of characters and that their stationary characters (on which the observer focuses) imply that all other characters do not change.
Primitive species: as with living ancestor, a term that does not make sense because any species is a mosaic of ancestral and derived character states [12], a product of the same range of evolutionary changes as all other extant taxa. A species cannot be all 'primitive' even if a particular character is described as such.
Relict: either geographical or phylogenetic, a species or a group of species remaining from a large group that is mainly extinct; there are no constraints on the time frame and extinctions can date to either the Holocene or the Palaeocene.

*Corresponding author:* Grandcolas, P. (pg@mnhn.fr).

CrossMark

Box 1. Defining relicts

'Relict' means 'remaining', implying a remnant of something formerly larger [14,47,72]. A phylogenetic relict represents the remains of a larger group of organisms, most taxa of which are now extinct (Figure IA). A geographical relict represents remains from a larger distributional area (Figure IB). A phylogenetic relict (sometimes called a 'numerical relict') is commonly a geographical relict and vice versa, as a function of the frequent allopatric distribution of species. Therefore, a relict is defined by the absence of many relatives that are supposed to be extinct.

This definition has often become confused by the use of less appropriate terms such as living fossil, which are often conflated with the term relict. 'Living fossil' is typically applied to groups that have been abundantly documented in the fossil record but are now represented by only a few extant species and where characters are assumed to have been 'fossilised' so that they have remained unchanged through time (e.g., ginkgos, coelacanths, platypus [20,73,74]). Similarly, the term 'phylogenetic relict' has been misleadingly used for old and small groups resulting from low speciation and

extinction rates, by contrast with the term numerical relict for old and large groups that have experienced extinction (e.g., [14,75]). This is an unhelpful restriction of the term relict, in contradiction to the common-sense meaning of the term as a remnant of something larger.

Although definition by absence is always a problem in science, there are three criteria that can be used to characterise relicts, and they work best in combination: (i) the fossil record can document extinctions if it is reasonably complete for the study group [76]; (ii) if the distribution area of the relict is much smaller or extremely disjunct relative to the area of its sister group, without evidence for origin by dispersal [56,77]; and (iii) if the molecular tree has a shape possibly indicating extinctions, supporting the hypothesis that the relict taxon is at the tip of a 'true' long branch [14,22,78]. The detection of past extinction is more speculative when the fossil record is deficient in space and/or time [79,80]. Placement of long branches on molecular trees is sensitive to the reconstruction method used (i.e., long-branch attraction [81]) or might imply a long period of evolution or an elevated rate of molecular evolution [82].
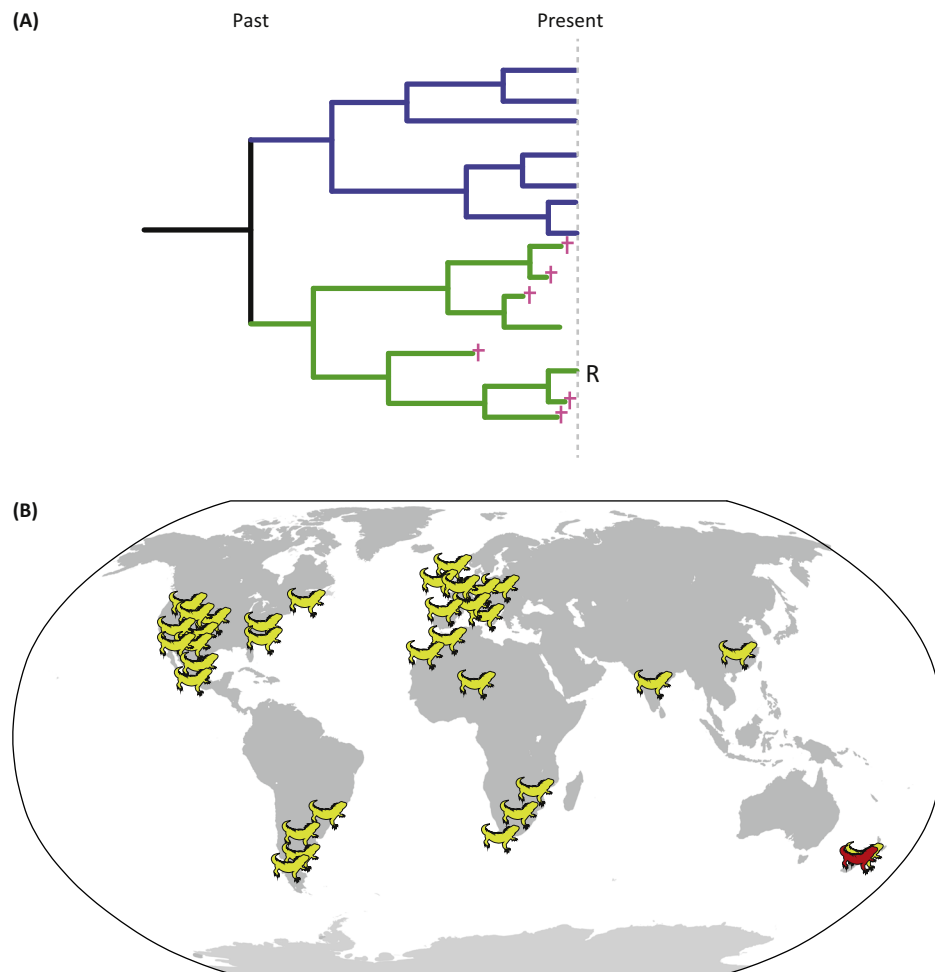
TRENDS in Ecology & Evolution

Figure I. The nature of a relict. **(A)** A phylogenetic relict (R) remains from a formerly large group of species, most of which are now extinct (†). **(B)** A geographical relict (red icon) remains from a larger former distributional area (yellow icons). As species in a clade are often distributed allopatrically, their extinction results in both increased branch length, leading to the relict, and decreased distribution. For example, the Rhynchocephalia (Sphenodontia) are represented by a single taxon (the tuatara *Sphenodon punctatus*) found only in New Zealand that is sister to all other squamate reptiles [7]; however, although the fossil record is patchy in space and time, it conservatively demonstrates a much wider former distribution of the order and does not directly inform us on the age of Sphenodontia in New Zealand.

survivors of clades with a large proportion of extinct members (Box 1), which tends to render them peculiar compared with other extant taxa. Such peculiarity makes them misleadingly judged to be closer than are others to

the clade ancestor and, therefore, considered as missing links or even living ancestors (see Glossary) [15–19]. In phylogenetic terms, character states observed at branch tips are attributed to basal nodes without justification.

The scientific literature is replete with papers intent on reconstructing the ancestors of charismatic groups of organisms and elucidating their combinations of character states (e.g., [3,4,20]). The approach, which itself appears to be a relict from earlier times, is to treat a relict taxon as a missing link to show intermediate character states and to help understand major evolutionary transitions. This is misleading in two ways. First, given the implied large-scale extinctions associated with relicts, there are many possible complete topologies that include the extinct taxa in which the relict could be variously placed (Box 2). Most of these complete topologies would not imply that the

---

Box 2. Inferring ancestral area

The tree *Amborella trichopoda* has characters that set it apart from other flowering plants but has no fossil record. Molecular phylogenetics indicates that it is sister to all other extant flowering plants (Figure I), but this does not directly demonstrate which of the character states (including location) it expresses are ancestral and which are derived (Figure II). *A. trichopoda* has been used prominently to better understand the ancestral characters of angiosperms (e.g., [4,5,69]). From this point of view, it has an archaic wood with a poor vessel-like structure and relatively ancestral reproductive characters. However, *A. trichopoda* also has a genome plastid that is massively transferred from other plants [28]. The lack of fossils means that there is no confirmation of either the ancestral status of the morphological characters or its former geographic distribution. The island of New Caledonia, the only place where *A. trichopoda* grows naturally, has long been viewed as a Gondwanan territory that separated from Australia 80 Mya as part of Zealandia [11,52] and local supposed relicts were interpreted as autochthonous remnants of Gondwanan biota [8]. An apparently parsimonious inference is that *A. trichopoda* has its origins in New Caledonia in the southwest Pacific and that this indicates that the New Caledonian biota is generally 'ancient' [6]. However, geological evidence precludes the long-term existence of *A. trichopoda* (or other terrestrial lineages) in New Caledonia (Figure III) [11].

A biogeographical study of the *A. trichopoda* situation, although preserving logical independence between biological and geological interpretations [55], must take into account that extinction in the Amborellaceae might have obscured the origin of the presence of *A. trichopoda* in New Caledonia. In the absence of fossils, one can only suggest that the Amborellaceae occurred widely outside New Caledonia 80 Mya, before becoming extinct in New Caledonia, if they occurred there, and then recolonising the island early shortly before extinction everywhere else. Clearly, falsifying such a complicated model would require studying *A. trichopoda*

diversity in New Caledonia to infer the age of the species and searching for fossils in other territories, but it could remain intractable.
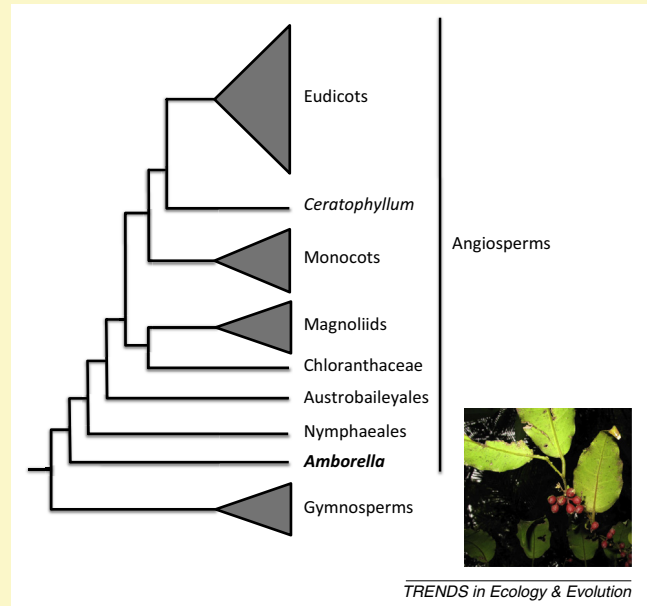

TRENDS in Ecology & Evolution

Figure I. Phylogenetic placement of *Amborella trichopoda* derived from molecular data representing extant lineages. Adapted, from [4,83]. Photograph by Jean-Noël Labat, MNHN.
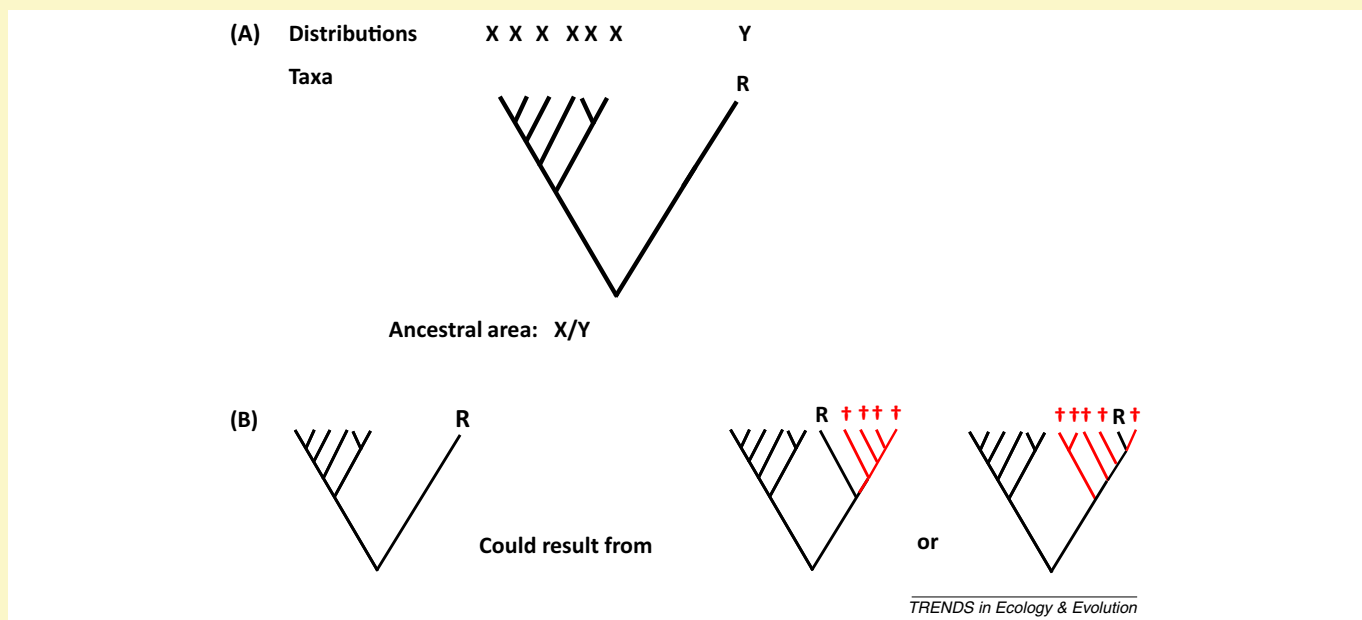

TRENDS in Ecology & Evolution

Figure II. Using a relict for evolutionary inferences. **(A)** Inferring the ancestral area (X/Y) of a clade might overemphasise the information provided by the relict (area X) and neglect the missing information from extinct species. **(B)** A present-day early-branching relict species might have been nested within an extinct clade or be relatively early branching in this clade (red branches indicate extinct lineages). Many different topologies can be implied by poor sampling of present-day forms and none of the alternatives can be excluded. As a result, phenotypic characters (whether distributional, morphological, or behavioural) cannot be determined as either 'ancestral' or 'derived'.
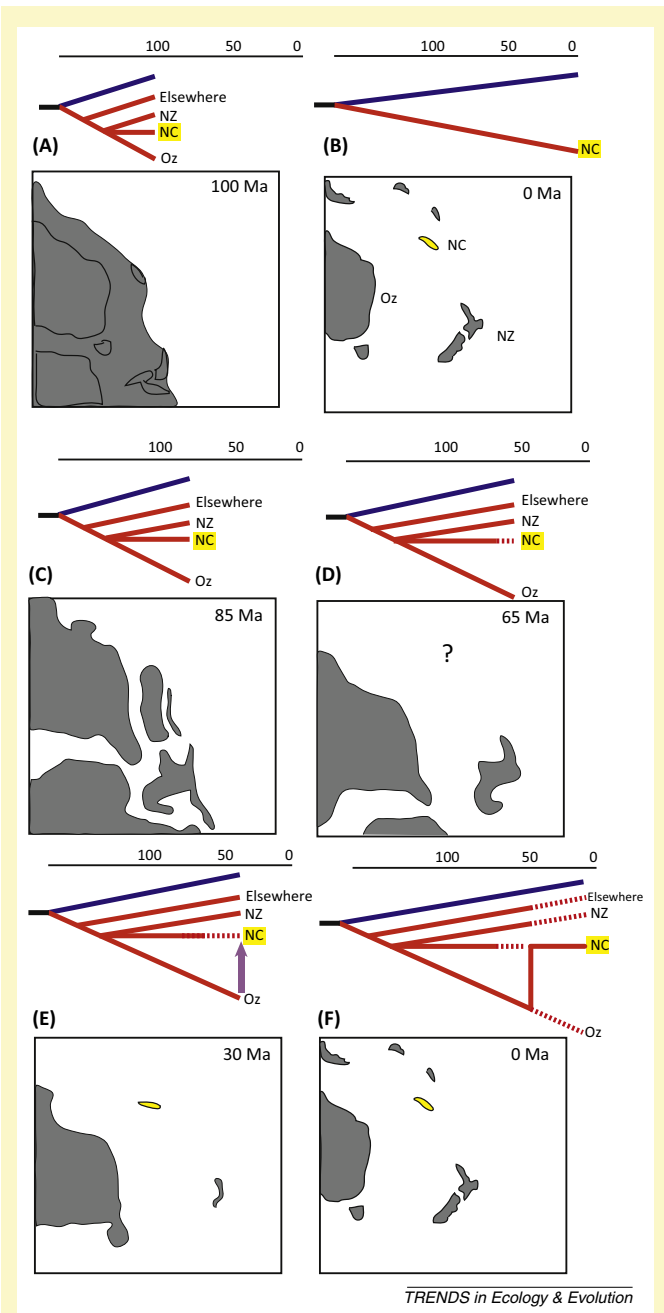
Figure III. Approximate palaeogeography of the New Caledonia region. The timescale is in millions of years, the red branches represent hypothetical 'Amborella' lineages, and the blue branch represents other angiosperms. One hundred million years ago, 'Amborella' was probably represented in many places by many lineages [New Caledonia (NC), New Zealand (NZ), Australia (Aus), and 'Elsewhere'] (A), but modern observation shows only one (B) in New Caledonia. However, any initial NC Amborella lineage (C) must have been lost during the Eocene (D), regained (purple arrow) during the Oligocene (E), and subsequently extinguished in other places. This complex order of events (F) involving the biogeographical equivalent of horizontal transfer is invisible in the phylogeny built from extant taxa (Figure I). Maps redrawn Adapted, with permission, from [84].

(*Ginkgo* spp.) are assumed to have remained unchanged since the Cretaceous [80 million years ago (Mya)], but have reproductive and growth characters that are at odds with the riparian habitats of their Cretaceous and Cenozoic ancestors [23]. The tuatara (*Sphenodon* spp.), the only representatives of the early branching lepidosaurian group Sphenodontia, are often taken as proof of the antiquity of the biota of New Zealand [7]; however, the genus shows the highest rate of molecular change recorded in vertebrates, as inferred from comparisons between sub-fossil and modern individuals [24]. The monotreme platypus (*Ornithorhynchus anatinus*) is expected to have a mix of reptile and mammal characters, but its venom has evolved convergently with that of both groups [3]. Coelacanth fish were thought to evolve so slowly that present-day *Latimeria* were thought to be similar to the numerous fossil Devonian Actinistia lobe-fin fish; however, these fossils are more diverse than previously assumed and modern *Latimeria* populations do not show low genetic diversity [24–26]. The early fossil opossum *Pucadelphys andinus* has been interpreted as being social, a behaviour that is unknown in present-day opossums [27]. *Amborella trichopoda*, the sister taxon to all other flowering plants that is commonly used to infer characters ancestral to angiosperms, has a plastid genome massively transferred from other plants [28]. Plants of the family Winteraceae lack xylem vessels; however, this is not an ancestral character but rather a secondary adaptation to freezing environments [29].

Is there a way to improve the evolutionary information provided by relicts about the ancestral characters of the clade? Methods of reconstruction of ancestral character states, [14,30–34] refer to both tree topology and branch length to compute ancestral states and thus can take into account extinction effects by considering more probable changes on the long branch of the phylogenetic tree leading to the so-called relict species. These methods can, however, be negatively affected by unknown character states that are absent in any of the present species of the clade under study but were present in the mainly extinct clade [2]. Other insights could be provided by comparing evolutionary rates for selected sets of characters in a clade comprising a relict, its sister-group, and various outgroup taxa, to conduct real tests of conservatism assumptions commonly associated with relicts. Information about character state evolution could potentially be explored in more detail using this type of approach if a detailed and well-attributed fossil record for the groups in question is also available.

Relicts do not imply permanence of biota

The same source of misunderstanding with relicts applies to biogeography. Here, distributional characteristics of the extant relict (i.e., its location) are also attributed to the extinct ancestors of that lineage [35]. Typically, biogeographical interpretation by optimisation of distribution area onto the tree featuring the relationships of extant taxa implies that the relict species, appearing as the sister group of the remainder, has remained in an area and is considered potentially ancestral – the so-called 'centre of origin' (Box 2) [6–8,36,37]. The unverified assumption is

character states of the relict were ancestral to the clade of interest. Second, if the evolutionary transition was abrupt, the search for a missing link as an evolutionary intermediate is irrelevant [21,22].

Relicts spuriously taken as missing links or living ancestors are often found to express remarkably derived characters [18]. For example, the present-day ginkgos

that the relict, confused with an old taxon, has remained at the location of the ancient centre of diversity of the clade or even the explicit place of a supposed centre of origin. This inference is thought to be justified as it applies the parsimony criterion by seemingly minimising the number of extinction and/or dispersal events required to explain the present-day pattern [8]. This assumption can be seen to be wrong when extinct taxa can be studied using an abundant fossil record. The true history then appears very complicated, with many extinctions and ultimate survival in only one place, which differs from the scenarios inferred when the present-day taxon is considered alone. Inferring the ancestral area for a clade is already difficult without the added deficiency caused by large-scale extinction [38–41]. Interpretation becomes impossible when dealing with areas that are not included with the sample of extant species.

From an ecological point of view, relicts are often seen as local survivors that remain either in patchy landscapes or on islands, following fragmentation of the ecosystem [42,43]. This approach pervades studies of glacial relicts, which are considered mostly as isolated, marginal, and remnant populations [44,45], often without a phylogenetic context. Interpretation in this way should be explicitly coupled with phylogenetic or genetic analysis of these populations, because a marginal or isolated population is not necessarily a geographical or even a phylogenetic relict but might result from colonisation of a distant area after dispersal.

The relict is often taken as a strong and emblematic indication of biotic permanence in continental islands, diversity centres (e.g., [6–8]), caves [46], or deep-sea marine environments (e.g., [37]). The assumption that such places can be modelled as museums of evolution (i.e., as though present-day high local diversity resulted from local high net speciation rates during long periods of evolution) has been questioned [10,11,47–54]. The mistaken rationale is that an 'old place' shelters 'old' taxa and thus that each is evidence of the other (e.g., [8]). However, this circular reasoning provides no testing power because the evidence for the hypothesis and the test are the same [55]. In this confusing situation, molecular dating and fossils are used to determine whether some emblematic and relict-like groups are older than the islands on which they are found. An inferred lineage age that is older than the island is often taken as evidence that the island is equally old and has existed with an intact permanent biota (e.g., [7,56,57]). Sometimes, this requires *ad hoc* solutions to reconcile conflicting information, such as invoking local 'hopping' among now-submerged islands or unrealistic rates of molecular evolution (e.g., [6,8]). Such approaches must be used carefully because lineage dating can be affected by poor sampling if the group is a relict [10,11,52]. For example, an old age can be obtained for a group that is represented by only one relict species, confusing the ages of the lineage and the age of the crown group.

However, relicts do not only represent poor samples for the groups that are studied locally, but also need to be considered at a larger taxonomic or geographical scale, larger than the clade or the distribution of the present-day relict species. In that widened perspective, one would consider any neighbouring area to generally also harbour some so-called 'relict taxa' from the same periods. In the southwest Pacific region, for example, the tuatara *S. punctatus* [24], sister to all extant squamate reptiles, branches early during the evolution of the Reptilia [7] (Box 1), New Caledonia shelters *Amborella trichopoda*, the sister group to all other flowering plants (no known fossil relatives) [27] (Box 2), and Australia harbours *Mastotermes darwiniensis*, the sister group to all other termites [58] (Box 3). Remarkably, despite being neighbours with a shared geological history, none of these areas shares any of these relicts. This puts into a more reasonable perspective any hypothesis of local biotic permanence in any of these areas when considered in isolation with a focus on the group of the relict of interest.

Relicts are not all the same

Four theoretical scenarios can be distinguished by considering relicts in the context of the mainly extinct group to which they belong. (i) Compared with the ancestor of the group, relicts could have the same state of the character of interest (e.g., with the same geographical distribution). (ii) Relicts could also differ from the ancestor of the group, having a derived character state, such as a different and disjunct distribution. On the time axis, relicts could be younger than (iii) or as old as (iv) the clade, depending on whether their lineage branched early or late within the extinct clade. Thus, some complex and unexpected situations could have occurred that are never considered *a priori*, such as a relict being either geographically distant but as old as the extinct clade or geographically close and younger than the extinct clade. A relict that is confirmed as geographically distant but as old as the extinct clade could possibly inform us about ancestral character states if it is

---

Box 3. Identifying a relict

A well-characterised relict is known among termites (Figure I). *Mastotermes darwiniensis* is the sole living representative of the early-branching family Mastotermitidae, the sister group to the remaining termite families [58]. The family is today restricted to northern Australia and *M. darwiniensis* has interesting morphological and social features [58,85]. Inferences about the origin of termites, which are all eusocial, has been mostly developed from comparison with cockroaches, especially those that perform brood care and feed on dead wood [85]. *M. darwiniensis* has therefore been interpreted as being closer to such cockroaches than to some other termites. On the one hand, some characters expressed by *M. darwiniensis* are seen as archaic and blattoid, such as an ootheca-like egg mass similar to its cockroach relatives, fully winged reproductives without a basal suture that enables wing loss after the nuptial flight, and fat-body bacteroid symbionts more similar to those of cockroaches than to those of other termites. On the other hand, *M. darwiniensis* shows many derived and original characters such as a true worker caste instead of developmentally flexible individuals supposedly ancestral to termites, a multiflagellate spermatozoid unique in animals, and an unspecialised feeding behaviour for processing humus as well as dead wood [58,86,87].

Although *M. darwiniensis* now occurs only in Northern Australia, Eocene fossils of the family have been found on most continents; an abundant fossil record, including beautifully preserved specimens in amber, shows that the group was distributed worldwide during the Eocene [88]. The current distribution can therefore be interpreted based on a worldwide extinction of the family in all areas except in Northern Australia.
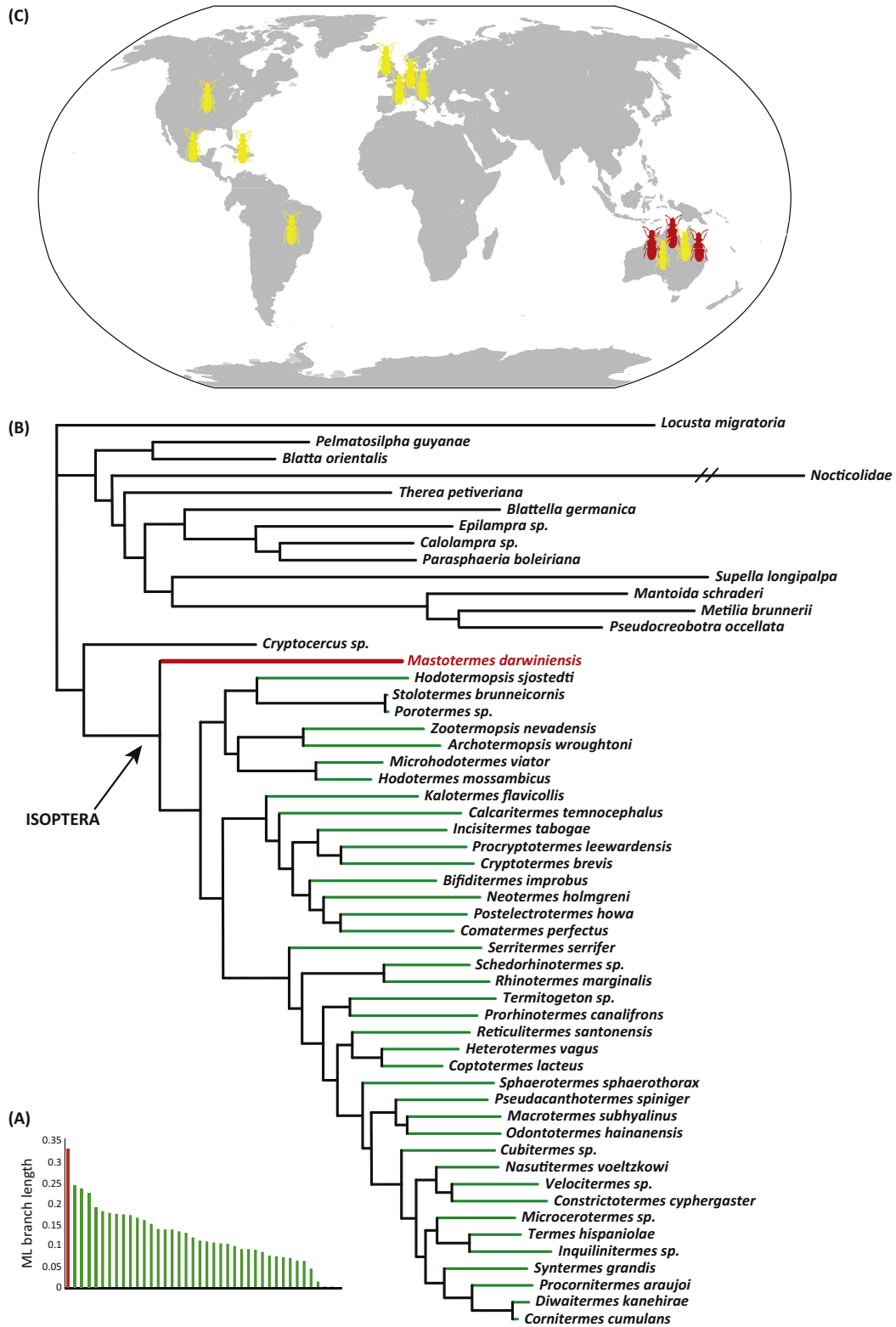
Figure I. Termite phylogeny based on Bayesian analysis of seven molecular markers [58]. **(A)** The northern Australian *Mastotermes darwiniensis* at the tip of the longest (red) branch in the tree, as shown in **(B)**, is phylogenetic sister to the remainder of the termites (green). **(C)** Numerous fossil Mastotermitidae species cannot be placed onto the molecular tree but testify to the former worldwide diversity of this group (yellow icons) compared with the extant *M. darwiniensis* in northern Australia (red icon) [88].

old enough to be deeply rooted in the tree. A geographically close but young relict will be more informative from a biogeographical point of view and could plausibly be used to understand the local permanence of that group.

The only way to distinguish among the four possibilities is to increase sampling in the supposedly homogeneous relict taxon in the hope of discovering genetic diversity that can be used to disentangle the origin of this taxon from the

old phylogenetic origin for the whole group inferred by the early branching. By contrasting the age of the crown group with the age of the stem group, some relicts could be better placed on the time axis. On the phenotype–space axis, the situation cannot be improved except with the help of a substantial fossil record that might demonstrate either unusual character states or combinations of character states or a different geographical distribution (e.g., [57]). In most instances, extant relict diversity is too pruned and the fossil history too scanty to enable informed interpretation.

What do relicts mean?

It might seem that relict species are only poor historical samples that are of no use in evolutionary biology and biogeography. However, they are useful in helping to address the question of extinction, and consideration of a relict within a molecular phylogeny permits estimation of extinction rates [59–61]. Relicts might provide indicators of the potential characters that enabled some taxa to survive regional or lineage extinctions and also serve as tests of whether extinction is purely stochastic. Niche modelling on relict species placed in the perspective of environmental change could help to elucidate why they survived, by distinguishing among several *ad hoc* scenarios [62–65]. Is the relict a generalist species bet-hedging in a changing environment or a specialist locally remaining in a small but stable refuge [9,66]? However, such a framework will be easier to apply when dealing with recent relicts [45] than with relicts of Palaeozoic or Cenozoic diversifications that have survived through a series of different environmental crises.

Relicts are also worth considering from the perspective of conservation biology [67,68]. They tend to be highly distinctive taxa in the modern biota, representative not of ancestral character sets or geographical distributions but of larger groups that have partly disappeared. From this point of view, they could be strongly informative about past diversity and have a high patrimonial value [45,53,69–71]. As we have emphasised, relicts are more informative in terms of the diversity of existing groups than in terms of original ancestral characters. This will be increasingly important in the coming decades as the major extinction crisis that is currently under way will make it necessary to conserve species not only for ecological services but also as representatives of a patrimony nested in the Tree of Life. Relicts, by their peculiarity, represent especially valuable taxa in this respect.

Concluding remarks

Relicts have been used in a 'gradist' perspective to detect supposed ancestral characters including areas and to validate assumptions of evolutionary stasis or biotic permanence in conjunction with misleading concepts of 'basal' or 'living fossil' species. Such an approach infers too much from too few data. Relicts should instead be studied to better understand regional and clade extinctions and should be conserved as representatives of large and mainly extinct groups. Regional biotas should not, therefore, be viewed as intact museums of biodiversity.

References

1 Heath, T.A. *et al.* (2008) Taxon sampling affects inferences of macroevolutionary processes from phylogenetic trees. *Syst. Biol.* 57, 160–166

2 Crisp, M.D. *et al.* (2011) Hypothesis testing in biogeography. *Trends Ecol. Evol.* 26, 66–72

3 O'Brien, S.J. (2008) The platypus genome unravelled. *Cell* 133, 953–955

4 Soltis, D.E. *et al.* (2002) Missing links: the genetic architecture of flower and floral diversification. *Trends Plant Sci.* 7, 22–31

5 Friedman, W.E. and Ryerson, K.C. (2009) Reconstructing the ancestral female gametophyte of angiosperms: insights from *Amborella* and other ancient lineages of flowering plants. *Am. J. Bot.* 96, 129–143

6 Ladiges, P.Y. and Cantrill, D. (2007) New Caledonia–Australian connections: biogeographic patterns and geology. *Aust. Syst. Bot.* 20, 383–389

7 Jones, M.E.H. *et al.* (2009) A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and palaeobiogeography of the tuatara (*Sphenodon*). *Proc. R. Soc. B* 276, 1385–1390

8 Heads, M. (2009) Globally basal centres of endemism: the Tasman–Coral Sea region (south-west Pacific), Latin America and Madagascar/South Africa. *Biol. J. Linn. Soc.* 96, 222–245

9 Goldberg, E.E. *et al.* (2005) Diversity, endemism, and age distributions in macroevolutionary sources and sinks. *Am. Nat.* 165, 623–633

10 Wallis, G.P. and Trewick, S.A. (2009) New Zealand phylogeography: evolution on a small continent. *Mol. Ecol.* 18, 3548–3580

11 Grandcolas, P. *et al.* (2008) New Caledonia: a very old Darwinian island? *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 363, 3309–3317

12 Hennig, W. (1966) *Phylogenetic Systematics*, University of Illinois Press

13 Engelmann, G.F. and Wiley, E.O. (1977) The place of ancestor–descendant relationships in phylogeny reconstruction. *Syst. Zool.* 26, 1–11

14 Brooks, D.R. and McLennan, D.A. (2002) *The Nature Of Diversity. An Evolutionary Voyage of Discovery*, University of Chicago Press

15 Crisp, M.D. and Cook, L.G. (2005) Do early branching lineages signify ancestral traits? *Trends Ecol. Evol.* 20, 122–128

16 O'Hara, R.J. (1992) Telling the tree: narrative representation and the study of evolutionary history. *Biol. Philos.* 7, 135–160

17 Krell, F.T. and Cranston, P.S. (2004) Which side of the tree is more basal? *Syst. Entomol.* 29, 279–281

18 Jenner, R.A. (2006) Unburdening evo–devo: ancestral attractions, model organisms, and basal baloney. *Dev. Genes Evol.* 216, 385–394

19 Gregory, T.R. (2008) Understanding evolutionary trees. *Evol. Educ. Outreach* 1, 121–137

20 Zhou, Z.Y. and Zheng, S.L. (2003) The missing link in *Ginkgo* evolution – the modern maidenhair tree has barely changed since the days of the dinosaurs. *Nature* 423, 821–822

21 Michener, C.D. (1985) From solitary to eusocial: need there be a series of intervening species? *Fortschr. Zool.* 31, 293–305

22 Pagel, M. *et al.* (2006) Large punctuational contribution of speciation to evolutionary divergence at the molecular level. *Science* 314, 119–121

23 Royer, D.L. *et al.* (2003) Ecological conservatism in the 'living fossil' *Ginkgo*. *Paleobiology* 29, 84–104

24 Hay, J.M. *et al.* (2008) Rapid molecular evolution in a living fossil. *Trends Genet.* 24, 106–109

25 Casane, D. and Laurenti, P. (2013) Why coelacanths are not 'living fossils'. *Bioessays* 35, 332–338

26 Friedman, M. and Coates, M.I. (2006) A newly recognized fossil coelacanth highlights the early morphological diversification of the clade. *Proc. R. Soc. B* 273, 245–250

27 Ladevèze, S. *et al.* (2014) First evidence of sexual dimorphism and gregariousness in an early metatherian population. *Nature* 474, 83–86

28 Rice, D.W. *et al.* (2013) Horizontal transfer of entire genomes via mitochondrial fusion in the angiosperm *Amborella*. *Science* 342, 1468–1473

29 Feild, T.S. *et al.* (2002) Hardly a relict: freezing and the evolution of vesselless wood in Winteraceae. *Evolution* 56, 464–478

30 Grandcolas, P. and D'Haese, C. (2003) Testing adaptation with phylogeny: how to account for phylogenetic pattern and selective value together? *Zool. Scr.* 32, 483–490

31 Mooers, A.O. and Schluter, D. (1999) Reconstructing ancestor states with maximum likelihood: support for one- and two-rate models. *Syst. Biol.* 48, 623–633

32 Pagel, M. and Meade, A. (2004) A phylogenetic mixture model for detecting pattern-heterogeneity in gene sequence or character-state data. *Syst. Biol.* 53, 571–581

33 Galtier, N. (2001) Maximum-likelihood phylogenetic analysis under a covarion-like model *Mol. Biol. Evol.* 18, 866–873

34 Penny, D. *et al.* (2001) Mathematical elegance with biochemical realism: the covarion model of molecular evolution. *J. Mol. Evol.* 53, 711–723

35 Santos, C.M.D. (2007) On basal clades and ancestral areas. *J. Biogeogr.* 34, 1470–1471

36 Edwards, S.V. and Boles, W.E. (2002) Out of Gondwana: the origin of passerine birds. *Trends Ecol. Evol.* 17, 347–349

37 Van Dover, C.L. *et al.* (2002) Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* 295, 1253–1257

38 Bremer, K. (1992) Ancestral areas – a cladistic reinterpretation of the center of origin concept. *Syst. Biol.* 41, 436–445

39 Ronquist, F. (1994) Ancestral areas and parsimony. *Syst. Biol.* 43, 267–274

40 Sanmartin, I. *et al.* (2008) Inferring dispersal: a Bayesian approach to phylogeny-based island biogeography, with special reference to the Canary Islands. *J. Biogeogr.* 35, 428–449

41 Ree, R.H. and Smith, S.A. (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst. Biol.* 57, 4–14

42 Watson, D.M. (2002) A conceptual framework for studying species composition in fragments, islands and other patchy ecosystems. *J. Biogeogr.* 29, 823–834

43 Hampe, A. and Jump, A.S. (2011) Climate relicts: past, present, future. *Annu. Rev. Ecol. Evol. Syst.* 42, 313–333

44 Woolbright, S.A. *et al.* (2014) Climate relicts and their associated communities as natural ecology and evolution laboratories. *Trends Ecol. Evol.* 29, 406–416

45 Habel, J.C. and Assmann, T., eds (2010) *Relict Species: Phylogeography and Conservation Biology*, Springer

46 Assmann, T. *et al.* (2010) The dark side of relict species biology: cave animals as ancient lineages. In *Relict Species: Phylogeography and Conservation Biology* (Habel, J.C. and Assmann, T., eds), pp. 91–103, Springer

47 Cronk, Q.C.B. (1992) Relict floras of Atlantic islands: patterns assessed. *Biol. J. Linn. Soc.* 46, 91–103

48 Desutter-Grandcolas, L. (1997) Studies in cave life evolution: a rationale for future theoretical developments using phylogenetic inference. *J. Zool. Sys. Evol. Res.* 35, 23–31

49 Gibert, J. and Deharveng, L. (2002) Subterranean ecosystems: a truncated functional biodiversity. *Bioscience* 52, 473–481

50 Little, C.T.S. and Vrijenhoek, R.C. (2003) Are hydrothermal vent animals living fossils? *Trends Ecol. Evol.* 18, 582–588

51 Yoder, A.D. and Nowak, M.D. (2006) Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annu. Rev. Ecol. Evol. Syst.* 37, 405–431

52 Trewick, S.A. *et al.* (2007) Hello New Zealand. *J. Biogeogr.* 34, 1–6

53 Fjeldså, J. and Bowie, R.C.K. (2008) New perspectives on the origin and diversification of Africa's forest avifauna. *Afr. J. Ecol.* 46, 235–247

54 Murienne, J. (2009) Testing biodiversity hypotheses in New Caledonia using phylogenetics. *J. Biogeogr.* 36, 1433–1434

55 Waters, J.M. and Craw, D. (2006) Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. *Syst. Biol.* 55, 351–356

56 Giribet, G. and Boyer, S. (2010) 'Moa's Ark' or 'Goodbye Gondwana': is the origin of New Zealand's terrestrial invertebrate fauna ancient, recent, or both? *Invert. Syst.* 24, 1–8

57 Biffin, E. *et al.* (2010) Did kauri (*Agathis*: Araucariaceae) really survive the Oligocene drowning of New Zealand? *Syst. Biol.* 59, 594–601

58 Legendre, F. *et al.* (2008) The phylogeny of termites (Dictyoptera: Isoptera) based on mitochondrial and nuclear genes: implications for and the evolution of the worker and pseudergate castes, and foraging behaviors. *Mol. Phylogenet. Evol.* 48, 615–627

59 Nee, S. *et al.* (1994) Extinction rates can be estimated from molecular phylogenies. *Philos. Trans. R. Soc. Lond. B: Biol. Sci.* 344, 77–82

60 Rabosky, D.L. (2009) Heritability of extinction rates links diversification patterns in molecular phylogenies and fossils. *Syst. Biol.* 58, 629–640

61 Crisp, M.D. and Cook, L.G. (2009) Explosive radiation or cryptic mass extinction? Interpreting signatures in molecular phylogenies. *Evolution* 63, 2257–2265

62 Graham, C.H. *et al.* (2006) Habitat history improves prediction of biodiversity in rainforest fauna. *Proc. Natl. Acad. Sci. U.S.A.* 103, 632–636

63 Carnaval, A.C. *et al.* (2009) Stability predicts genetic diversity in the Brazilian Atlantic Forest hotspot. *Science* 323, 785–789

64 Murienne, J. *et al.* (2009) Species diversity in the New Caledonian endemic genera *Cephalidiosus* and *Nobarnus* (Insecta: Heteroptera: Tingidae), an approach using phylogeny and species distribution modelling. *Biol. J. Linn. Soc.* 97, 177–184

65 Grandcolas, P. *et al.* (2011) Mapping extrinsic traits such as extinction risks or modelled bioclimatic niches on phylogenies: does it make sense at all? *Cladistics* 27, 181–185

66 Parsons, P.A. (2005) Environments and evolution: interactions between stress, resource inadequacy and energetic efficiency. *Biol. Rev. Camb. Philos. Soc.* 80, 589–610

67 Vane-Wright, R.I. *et al.* (1991) What to protect? Systematics and the agony of choice. *Biol. Conserv.* 55, 235–254

68 Forest, F. *et al.* (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* 445, 757–760

69 Pillon, Y. and Munzinger, J. (2005) *Amborella* fever and its (little) implication in conservation. *Trends Plant Sci.* 10, 519–520

70 Redding, D.W. *et al.* (2008) Evolutionarily distinctive species often capture more phylogenetic diversity than expected. *J. Theor. Biol.* 251, 606–615

71 Pellens, R. and Grandcolas, P., eds (2015) *Biodiversity Conservation and Phylogenetic Systematics: Protecting Species in a Major Extinction Crisis*, Springer–Verlag

72 Holmquist, C. (1962) The relict concept – is it a merely zoogeographical conception? *Oikos* 13, 262–292

73 Warren, W.C. *et al.* (2008) Genome analysis of the *Platypus* reveals unique signatures of evolution. *Nature* 453, 175–183

74 Amemiya, C.T. *et al.* (2010) Complete HOX cluster characterization of the coelacanth provides further evidence for slow evolution of its genome. *Proc. Natl. Acad. Sci. U.S.A.* 107, 3622–3627

75 Simpson, G.G. (1953) *The Major Features of Evolution*, Columbia University Press

76 Taylor, P.D. (2004) Extinction and the fossil record. In *Extinctions in the History of Life* (Taylor, P.D., ed.), pp. 1–34, Cambridge University Press

77 Sharma, P. and Giribet, G. (2009) A relict in New Caledonia: phylogenetic relationships of the family Troglosironidae (Opiliones: Cyphophthalmi). *Cladistics* 25, 279–294

78 Ward, P.S. *et al.* (2010) Phylogeny and biogeography of dolichoderine ants: effects of data partitioning and relict taxa on historical inference. *Syst. Biol.* 59, 342–362

79 Purvis, A. (2008) Phylogenetic approaches to the study of extinction. *Annu. Rev. Ecol. Evol. Syst.* 39, 301–319

80 Quental, T.B. and Marshall, C.R. (2010) Diversity dynamics: molecular phylogenies need the fossil record. *Trends Ecol. Evol.* 25, 434–441

81 Bergsten, J. (2005) A review of long-branch attraction. *Cladistics* 21, 163–193

82 Magallón, S. (2010) Using fossils to break long branches in molecular dating: a comparison of relaxed clocks applied to the origin of angiosperms. *Syst. Biol.* 59, 384–399

83 Soltis, D.E. *et al.* (2008) Origin and early evolution of angiosperms. *Ann. N. Y. Acad. Sci.* 1133, 3–25

84 Lee, D.E. *et al.* (2001) Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Aust. J. Bot.* 49, 341–356

85 Donovan, S.E. *et al.* (2000) Morphological phylogenetics of termites (Isoptera). *Biol. J. Linn. Soc.* 70, 467–513

86 Pellens, R. *et al.* (2007) The evolutionary transition from subsocial to eusocial behavior: phylogenetic and ecological evidence for modification of the 'shift-in-dependent-care' hypothesis with a new prototermite model. *Mol. Phylogenet. Evol.* 43, 616–626

87 Donovan, S.E. *et al.* (2001) Gut content analysis and a new feeding group classification of termites. *Ecol. Entomol.* 26, 356–366

88 Nel, A. and Paicheler, J.C. (1993) Les Isoptera fossiles: état actuel des connaissances, implications paléoécologiques et paléoclimatologiques (Insecta, Dictyoptera). *Cah. Paleontol.* 102–179