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Land bridge and long-distance dispersal ——Old views, new evidence

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Abstract The study of land bridge based on continental drift¹⁾ and long-distance dispersal are gaining increasing attention in biogeography. We review several major dispersal theories including the Malpigiacea route, patterns of chameleon dispersal and the floating island model. The Malpigiaceae route indicates that the Malpigiaceae family originated in northern South America and that members of several clades migrated into North America and subsequently moved via north Atlantic land connections into the Old World starting in the Eocene. This route may also explain many other pantropic disjunction patterns, including some Chinese plants disjunctions, involving South America. Not all biogeographical distribution patterns can be explained by vicariance theory, so more research, including chameleon distribution, has recently focused on long-distance dispersal. The latest analyses suggest that chameleons have dispersed over long-distances from Madagascar on several occasions. The floating island model would explain flora and fauna similarities between South America and Africa. Studying long-distance dispersal mechanisms is important for understanding distribution patterns and even the spread of pandemics. More research on the specific implications of longdistance dispersal for biogeography is necessary.

Keywords: bioogeography, continental drift, Land bridge, Malpigiacea route, Long-distance dispersal.

The theory of sea-floor spreading and continental drift is one of the most important achievements in the last century with large ramification for biogeography^[1]. Similarly, cladistics, which was started in the 1960s, has been widely employed in systematics research^[2]. The integration of the continental drift theory with cladistics gives rise to vicariance biogeography, which is popular in biogeographical research today. Distributions of monophyletic groups of taxa are explained by the reconstruction of area cladograms in vicariance biogeography; this has advanced biogeographical research in the 20th century [3-5]. While biogeographical research was deeply affected by these approaches, the use of the land bridge hypothesis to determine the origin of taxa was generally dismissed^[6]. Reven and Axelrod^[7] published their famous paper "Angiosperm biogeography and past continent movement" in which the distribution patterns of angiosperms were explained mainly by continental drift. Biogeographical studies were greatly influenced by this paper; after its publication the continental biogeographic disjunctions of plants and animals were mainly explained by vicariance biogeography^[8,9].

Nucleotide sequencing of taxa has become an important tool to trace phylogeny. It is possible to estimate the time of diversification of angiosperm clades using a molecular clock. Furthermore, estimates of the time of angiosperm origins are becoming more precise as greater numbers of important angiosperm fossils are found $\frac{[10-22]}{10}$. New data show that the diversification times of many plants are much later than previously thought; major diversification of angiosperms seem to have occurred in the Late Cretaceous and Early Paleocene^[23,24]. At this time, Pangaea had broken up and southern America and Africa were widely divided; the continents were close to their current positions, with the exception of India, which was still moving northwards^[25]. Based on this new information, continental disjunctions, such as the distribution patterns of Malpighiaceae, Chameleonidae subf. Chamaeleoninae, Burseraceae, Styraceae, cannot be explained by vicariance and continental drift^[23,26-28]. Land bridges must have played an important role in their current distribu-

¹⁾ Land bridge theory based on continental drift assumes that there are islands or island chains exsited between certain contients which forms as bridges for flora and fauna exchange. These islands or island chains are generally called "Land bridge". Followed with continent drift, position change of land and ocean, and variation of sea level, the position of these islands or island chains varies. Some of them even disappeared and lost its function as Land bridge. This is different from the other Land bridge theory which assumes that the position of the cotinents and Land bridges are fixed; it appeas and disappears with the variation of sea level.

tion patterns. Furthermore, there is no relationship between continental drift and the disjunction patterns of some later plant diversifications, such as the primarily woody Boraginales^[29] and *Kelloggia* (Rubiaceae)^[30]. New theories and method are needed to study these kinds of distribution patterns.

Recent research shows that long-distance dispersal (LDD), such as seed and fruit dispersal by animals, wind and oceans, plays an important role in creating distribution patterns and rich biodiversity^[29-34]. The existence of these typically rare events of LDD was recognized long ago by Darwin^[35]. LDD was considered unquantifiable, unpredictable, unimportant and random, especially between the 1960s and 1980s^[36]. However, LDD has recently attracted more attention, and papers on LDD increased rapidly in the last decade^[31]. Research into the mechanisms, events and media of LDD are more precise, and stronger LDD events were detailed and proven. Indeed, land bridge and LDD are becoming new hot spots in biogeography. These new trends in biogeography are reviewed in the current paper and we hope this can contribute implications for the biogeography.

1 Land-bridge based on continental drift——The Malpighiaceous route and Chameleon distribution

1.1 Malpighiaceous route

Pantropical disjunctions are the patterns in which taxa are distributed in tropical America, Africa and Asia. Euphorbiaceae, Burseraceae, Malpighicaceae, Lauraceae, Araceae and Piperaceae have this disjunct distribution, and in all about 120-angiosperm families display this pattern. Different explanations for these disjunctions were proposed. Wu et al. [37,38] explained these disjunctions based on the Pangaea hypothesis. Raven and Axelrod^[7] indicated the disjunctions of Lauraceae and Annonaceae resulted directly from migration between the continents when these regions were relatively close. Zhou^[39] proposed that Chloranthaceae originated from Southern Laurasia in the very early Cretaceous; at that time, Laurasia was still a complete continent and Gondwana had just started to breakup. Plants of Chloranthaceae could have easily dispersed to other continents from their origin via the plate movement. Vogel^[8] thought Malpighiaceae was widely distributed in Gondwana and moved to different continents with the breakup of Gondwana; the so-called Gondwanian aborigine hypothesis. However, Anderson^[40] proposed an

REVIEW

American colonist hypothesis to explain the same distribution pattern, suggesting that Malpighiaceae originated from northern South America, and crossed the Atlantic eastward to Africa to form the current distribution pattern. Recently, Davis *et al.*^[23] reinvestigated Malpighiaceae and proposed a Malpighiaceae route to explain the distribution pattern of Malpighiaceae. This route has significant implications for pantropical distribution patterns.

Davis *et al.*^[23] analyzed the phylogeny of Malpighiaceae using the *ndh*F sequences from *PHYC*. Their results are robust and congruent with previous parsimony analyses based on four chloroplast genes^[41,42]. These results indicate that the Malpighiaceae can be divided into two major clades. One is subfamily Byrsonimoideae, which is distributed in the New World tropical areas, and the other includes six linguages that are disjunctively distributed in both the New and Old World tropical areas. Within this clade, the Old World groups have winged-fruits. Reliable winged-fruit fossils of *Tetrapervs* were found from the Oligocene (33 Myr) in Hungary and Slovenia. The Oligocene was considered the divergence time of Tetraperys and its sister groups. Based on this divergence time and the length of the clade, it can be postulated through molecular clock theory that the Malpighiaceae originated 63.5±5.8 Myr ago. Furthermore, it seems that the divergence time of the six lineages distributed in New and Old World should be around the Early Eocene (55.1±6.0 Myr) and the Middle Miocene (12.9±0.85 Myr), when the African and American Continents separated (the latest time for this separation is about 105 Myr ago^[23]).

With the evidence from phylogeny, molecular theory and fossils, Davis *et al.*^[23] suggested that in the Early Paleocene (64 Myr), Malpighiaceae originated from northern South America, and members of several clades dispersed into North America and moved via North Atlantic land connections into Laurasia in the Eocene. Therefrom, the family spread to tropical Asia through Laurasia, during which some of the species dispersed to Africa via Europe and then to Madagascar (Fig. 1). We call this migration route the Malpighiaceous route, as it explains phylogentical relationships of groups of the Malpighiaceae, the occurrence of Malpighiaceous fossils in Europe, and the disjunct patterns of the Malpighiaceae. There are two fundamental geology questions related to the Malpighiaceae route. First, was dispersal possible between South and North American during Early Tertiary? Second, did the paleoclimate



Fig. 1. The bidirectional Malpighiaceae route^[23,271]. ..., Dispersal route of Malpighiaceae and Burseraceae; —, dispersal route of Lauraceae; \bigstar , hypothetic original points of Malpighiaceae; \blacksquare , fossil points of Malpighiaceae in Europe and Africa; \diamondsuit , fossil points of Burseraceae; \bigstar , hypothetic original points of Burseraceae; \blacklozenge , hypothetic original points of Burseraceae; \blacklozenge , hypothetic original points of Burseraceae.

suitable to the dispersal of Malpighiaceae exist in Laurasia? For the first question, studies on mammals of the Tertiary in Cuba and Puerto Rico suggested that South and North America could have been linked through land patches and volcanic islands^[43,44]. For the second question, it was also proved that during the Eocene the Atlantic land bridge played an important role in flora and fauna exchanges between North America and Euro-Asian continents^[45]. The existence of a "boreotropical" flora in Laurasia during the Eocene also provides evidence that the paleo-climate was suitable for the dispersal of Malpighiaceae^[7,23].

As far as the other two explanations for the Malpighiaceous disjuctions are concerned, the timing of Malpighiaceae origin computed by the molecular clock does not fit with the "Gondwanian aborigine" theory [8]: it should predate the separation of Africa and South America. Although the "American colonist hypothesis"^[40] agrees with the Malpighiaceae route on the place of origin, the route and method of dispersal are different. The "American colonist hypothesis" requires six long distance dispersals between South America and Africa. This hypothesis predicts that the ages of Malpighiaceae and of divergences between New and Old World lineages are younger than the last known connection between South America and Africa. It also cannot explain the occurrence of Malpighiaceae fossils in the north hemisphere and Africa during Eocene and Oligocene. The Malpighiaceae route not only explains the Malpighiaceae distribution patterns, but, most importantly, it provides a new way of explaining the disjunct pantropic distribution patterns. Moreover, the Malpighiaceae route also explains similar disjunct pantropic distributions of the Burseraceae^[27], Melastomeae of Melastomataceae^[46] and Lauraceae^[47]. The only difference among them is the place of origin. Burseraceae originated from southern North America, dispersed east to tropical Asia, south to South America, and entered Africa through Europe. Lauraceae originated from tropical Asia, spread west in Lauraisa and entered Africa through Europe, and South America from North America (Fig. 1).

1.2 Chameleon distribution

The distribution patterns and mechanisms of formation of many animal and plant groups that are disjunctively distributed in Africa and Madagascar are closely related with land bridge-based oceanic dispersal theory. The distribution of chameleons is a good example. Chameleonidae subf. Chamaeleoninae occur mainly in Madagascar and on the African continent, but they are also distributed in south Europe, the Middle East, India, Sri Lanka, and on islands such as the Seychelles and the Comoros. Based on morphology, chameleons can be divided into two major groups: (1) larger and predominantly arboreal chameleons, which are widely distributed; (2) the geographically restricted, smaller and mainly ground-dwelling dwarf chameleons. The dwarf chameleons can be further divided into two genera. One genus occurs on the African continent, and the other in Madagascar^[6]. Debates over the evolution history of chameleons mainly focus on whether the ground dwelling dwarf chameleons primitive, or descendent from arboreal ancestors, and whether chameleons originated in Madagascar, or on the African continent.

Three theories are proposed to explain chameleon distribution patterns; Gondwanan origin^[48,49], partial Gondwanan origin^[50], and post-Gondwanan origin^[26]. Cladistic analyses based on morphological characteristics suggest that chameleons originated in Gondwana, and the breakup of Gondwanan resulted in the chameleon distribution patterns. This forms the Gondwanan vicariance hypothesis^[48,49]. In order to test this hypothesis, Raxwarthy *et al.*^[26] studied up to 52 species, especially species from islands of Seychelles, the Comoros and Reunion, including all representative groups of Chameleonidae subf. Chamaeleoninae. Their work shows that Chameleonidae subf. Chamaeleoninae is monophyletic, based on an integrated analysis of three

gene fractions, i.e. mtDNA, NADH subunit 4 and adjacent transfers RNA, morphological characteristics and behaviors. The two basal clades (clades 1 and 2) on the molecular tree belong to genus *Brookesia*, which is dwarf and endemic to Madagascar. Amongst the rest, the so-called 'typical' chameleons, the two basal groups (*Rhampholeon* and *Bradypodion*) are endemic in Africa. Moreover, *Calumma tigris* distributed in Seychelles and *Ca. fallax* distributed in Madagascar are sister groups; *Chamaeleo zeykanicus* distributed in India and *Ch. Calytratus* distributed in Africa. Moreover, *Furcifer cephalolepis*, distributed Comoros, and *F. campani*, distributed in Madagascar, are sister groups (Fig. 2)^[26].

The chameleon fossil record is very poor, none earlier than the Miocene (23.7-5.3 Myr), when Gondwana had already broken up. Had chameleons originated from ancient Gondwana, and thence been distributed to Madagascar, India and the Seychelles, the time of the origin must be earlier than 165 Myr when Madagascar and India separated from Africa. Moreover, based on the molecular clock, the divergence time of chameleon is after the breakup of Gondwana. At the same time, no evidence supports the Gondwanan origin because the primitive group is not *Rhampholeon* and *Bradypodion*, which are distributed in Africa, but *Brookesia*, which is endemic to Madagascar.

Based on all the evidence, Raxworthy *et al.*^[26] suggested that chameleons originated from Madagascar after the breakup of Gondwana, followed by multiple "out-of-Madagascar" dispersal events to Africa, the

REVIEW

Seychelles and the Comoros archipelago; the post -Gondwanan theory. The distribution of chameleon on Comoros also supports the post-Gondwanan hypothesis because Comoros is a historically isolated volcanic island 300 km from Madagascar formed around 0.13-5.4 Myr. It is only possible that chameleons arrived here through an LDD across the sea. It is also proved though molecular trees that a cross-ocean LDD existed since Furcifer cephalolepi and F. polleni in Comoros are sister groups of F. campani in Madagascar. Moreover, the distribution of F. pardilis both in Madagascar and Reunion Island also proved the existence of natural transocean LDD, since the earliest records of human activities in Reunion only dated back to the 17th century. In addition, post-Gondwanian origin patterns also exist with cichlids, ants and turtles^[6]. Recent study by Vences^[51] on amphibians and other terrestrial vertebrates in Africa and Madagascar reveal that fauna exchanges between these areas in the Cenozoic were via dispersal across the ocean. A land bridge across the Mozambique Channel between the mid-Eocene and the Early Miocene^[6,52] was proposed to explain the disjunctive dispersal of these groups in Africa and Madagascar; however, more evidence is required to prove the existence of this land bridge.

2 Long distance dispersal and its possible mechanism

In order to explain cross-ocean dispersal, Darwin and Wallace proposed LDD^[35,53]. Up unto the mid 20th



Fig. 2. Maximum parsimonious tree of subf. Chamaeleoninae based on molecular and morphological charateristics. Taxon distribution: M, Madagascar; AF, Africa, Arabian Peninsula and Near-Middle East; SE, Seychelles; I, India, Pakistan and Sri Lanka; (C), Comoros; (R), Reunion. The species in rectangle with solid line are the dwarf chameleons (i.e. *Brookesia* spp.) The species in rectangle with broken line are "typical" chameleons. The species in rectangle with letter are sister groups^[26].

century, LDD was considered unquantifiable because of the lack of accountable evidence and explanations of the mechanisms. The disjunct distributions between continents was mainly based on vicariance theory $\frac{[36,54]}{}$. However, this theory cannot explain all disjunctions. Therefore, new attention has been directed towards LDD, particularly given the increased understanding of its mechanisms and its role in invasive in ecology and genetic diversity $\frac{[29-34,54-62]}{[29-34,54-62]}$. Typical examples are the pantropical disjunct distributions of primitive woody groups such as the Ehretiaceae, Cordiaceae and Heliotropiaceae. Continental drift and vicariance biogeography was initially considered responsible for this distribution pattern^[63]. However, Gottschling *et al.*^[29] showed that continental drift theory was incompatible with the divergence time of these groups according to the molecular clock and fossil evidence: other explanations are necessary. They suggested the distributions are most probably due to LDD, in which birds and small mammals would be the dispersal vectors. However, direct evidence of animal dispersal is still missing. Another example is the genus Kelloggia. It only contains two species, K. galioides and K. chinensis, distributed in west America and the Hengduan Mountains in China respectively. Nie et al.^[32] found that Kelloggia is monophyletic. Based on the molecular clock, the divergence time was 5.24±2.32 Myr (the beginning of Pliocene) when the pattern of modern continents had formed and the Atlantic land bridge had disappeared. The most reasonable explanation for the intercontinental disjunction in *Kelloggia*, is via animal vectors as the fruits of *Kelloggia* possess hooked bristles that are easily to be carried by birds and other animals.

Typical examples of LDD come from the work of Houle and Renner. Renner^[30] collected molecular biology data from 111 genera in 53 families, confirmed their monophyletic nature, and analyzed the possibility of LDD and dispersal media. This study identified 11 cross Atlantic dispersal types, amongst which, four are related to wind, six with sea current, and one remains unknown. Houle^[33,34] proposed the floating island model when trying to explain the disjunctive distribution of Paltyrrhine Monkeys, Caviomorph rodents and and *Mabuya* spp.

The first cave dwelling rodent fossils date to 32-34 Myr and the earliest Paltyrrhine to 26 Myr. These all have closely related groups in Africa, but no fossils were found in North America, Australia or Antarctica, which testifies to their cross Atlantic distribution^[33,64].

The floating island model is the best explanation of these animals' disjunctive continental distribution. In river deltas, large patches of land are commonly washed down and become floating islands. The biggest floating island recorded is around $60 \times 23 \text{ m}^2$, with trees as high as 15 m. This mode could have facilitated trans Atlantic dispersal in the past, because the historic sea current was similar to present, but the width of the Atlantic was much narrower. The shortest distance between South America and Africa increased from 1000 km in 50 Myr to 1900 km in 30 Myr. In addition, ocean drilling and sonar studies^[30] reveal that Rio Grande in the south Atlantic and Walvis Ridge in Africa were above sea level at least during Oligocene. The elevation of Rio Grande was equal to Rio de Janeiro in Brazil, and Walvis Ridge to the Cape of Good Hope. Favorable factors such as sea current and wind direction, make the actual sailing distance even shorter^[30,33]. Under the influence of sea currents and trade winds, it would take 7-11 d to cross the Atlantic in the Eocene, and 10-15d in the Oligocene. The survival duration of the animals mentioned above are around 13 days, thus it is possible for them to transit the Atlantic on floating islands $\frac{[33,34]}{[33,34]}$. Floating islands also provide the possible LDD mechanism for plants. Trees can act as sails on floating islands and provide habitat for animals. Small seeds, such as Melastomataceae can be preserved in the soil and dispersed^[30].

The floating islands model, however, does not provide a complete answer. For example, molecular biological evidence suggests that the Bromeliaceae dispersed from South America to Africa and formed a disjunctive distribution pattern around 8 Myr^[65], while Melastomataceae and Rapateaceae dispersed in a similar pattern in 11 Myr^[66] and 6 Myr^[65,67] respectively. No evidence shows whether floating islands facilitated these dispersal events. The most possible method of dispersal is by wind, but clear evidence of wind dispersal is hard to collect since there are large variations in wind power and velocity over time^[30].

There is no standard mechanism to explain all LDD patterns. In fact, studies show that LDD is the consequence of random events^[30]. For example, the Canadian species *Asarum canadense* multiplies mainly through asexual reproduction. Its seed dispersal is limited and dependent upon ant vectors. The maximum distance that an ant can carry is 35 m; hence theoretically, the maximum dispersal distance of *Asarum canadense* in the 16000 years since the ice age is 10-11 km. The

actual dispersal distance, however, is hundreds kilometers. Likewise, for understorey herbs in North America, the calculated dispersal distance is no more than 100 km; yet the actual dispersal distance is 450-2000 km. Present dispersal mechanisms cannot explain these theoretical and actual differences. They can only be explained by random events, such as cyclones, hurricanes or other phenomena^[56,57]. Moreover, although propagules may be transported by various mechanisms, LDD is not necessarily successful. A good example of this is Surtsey. Formed in 1967, Surtsey is an island of 2.7 km² 33 km off the coast of Iceland. Observation of dispersed seeds to this island found that few of the seeds are dispersed in fecal matter and 70% are transported by sea currents (among which only 25% were viable after water transportation)^[68].

3 Discussion

The factual acceptance of continental drift and the timing of the breakup and collision the continents is a geological basis for us to understand plant and animal distribution, no matter whether we are considering vicariance or dispersal biogeography. There is no doubt that vicariance biogeography plays important roles in the specialization, biodiversity conservation, biological coevolution and development of flora. Although vicariance has successfully explained the distribution pattern of many groups, it cannot solve all the problems. The distribution pattern of younger groups cannot be explained by vicariance biogeography. Land bridge and LDD are not new scientific theory, but added with rich new morphological and molecular evidences; they have been given new significance when considered in concert with continental drift^[31,54]. Sound scientific hypotheses can be developed when specific theories are applied to explain specific dispersal patterns based on particular divergence times for groups of ancient origin or higher levels (such as order, family and so forth). The disjunctions of Annonaceae and Illiciaceae, for example, can be explained by continent drift and vicariance biogeography. However, vicariance and continental drift cannot explain the biogeography of many late origin groups (e.g. Malpighiaceae and Burseraceae) or the disjunctions at genus or species levels $\frac{69}{2}$.

The Malpighiaceaous route provides a new way of explaining Asian-South American-Africa disjunctions. Acanthochlamydaceae is monotypic family distributed

REVIEW

in dry-warm valleys of the Hengduan Mountains of China, but Velloziaceae in South America and Africa is a closely related group^[37,70]. Since no agreement on the phylogeny was reached, there was no accountable explanation for this distribution pattern. However, after the phylogeny was confirmed by molecular evidence, the Malpighiaceaous route becomes the best hypothesis to explain its distribution pattern and phylogeny.

There are 3116 genera of seed plants in China, among which 316 genera are pantropically distributed, and 29 genera have a tropical Asia-tropical South America disjunctive distribution^[71]. There are various possible causes for these distribution patterns, but the Malpighiaceaous route is an important clue. Lardizabalaceae is a monophyltic family^[72] with a disjunct distribution across the Pacific, from the Himalayas to Japan, Myanmar and Indochina and temperate South America (west of the Andes). Fossils of Sargentodoxaceae, related to Lardizabalaceae, are also found in Europe and North America^[73-75]. As the distribution</sup> pattern of Lardizabalaceae is similar to that of Malpighiaceae, the Malpighiaceaous route also can be applied. Research by Wang¹⁾ suggested that Lardizabalaceae originated in the Late Jurassic (computed by molecular clock). Hence he explains its distribution pattern based on continental drift and vicariance biogeography: it originated in southern Laurasia, its descendants dispersed to Gondwana before the Pangea breakup; after Pangea broke up, Lardizabalaceae migrated to different continents. However, the molecular clock should be recalculated because it does not match with the known origins and divergence of angiosperms^[10,22]. Reinvestigating the divergence time of groups and referring to the Malpighiaceaous route could provide new ways of explaining the distribution pattern of Lardizabalaceae. In addition the Malpighiaceaous route could also help explain some of the south and north temperate disjunctive distribution patterns. There are around 30 species of Caltha disjunctively distributed in southern and northern temperate zones^[76]. The basal group of this genus is distributed in North America while its secondary clades are distributed in both South and North America. This reveals that this genus originated in North America, entered South America and then dispersed to the South Temperate Zone. The dispersal in the North Temperate Zone (i.e. into Euro-Asia) was via land bridge across what is now the Atlantic. This dis-

¹⁾ Wang Feng, 2002, The phylogeny and biogeography of Lardizabalaceae, PhD theses: Kunming Institute of Botany, CAS.

persal matches with the Malpighiaceaous route^[76], which is bidirectional and can explain the dispersal of groups that originated in modern continents, as well as disjunctively distributed groups that originated in ancient continents^[23]. Styracaceae originated in the Euro- Asian continent and forms a disjunct distribution across modern and ancient continents with this route $\frac{[28]}{2}$. This route is also proven to be an important conduit for global exchange of angiosperms in the Tertiary^[23,28,46,47,77–80]; therefore, more attention should be paid to this route in future biogeographic studies in China.

Although research on LDD mechanisms is moving rapidly, we are still accumulating information^[29–33,54,55,58]. It has been likened to a network of yellow brick roads under construction that lead to new and unknown worlds^[31]. LDD is a new trend in research field of biogeography. It is an opportunity as well as a challenge to carry the research on LDD, revealing its important role in biogeography, biodiversity conservation, invasive species and the dispersal of pandemic diseases.

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References

- Li J J, Fang X M. Uplift of the Tibetan Plateau and environmental changes. Chin Sci Bull, 1999, 44(23): 2117-2124
- 2 Henning W. Phylogenetic Systematics. Urbana: Univ Illinois Press, 1966
- Wiely E O. Phylogenefic systematics and vicariance biogeography. Syst Zool, 1988, 37: 271-290
- 4 Nelson G, Platnick N I. Sytematics and Biogeography: Cladistics and Vacariance. New York: Columbia Univ Press, 1981
- 5 Zhou M Z, Zhang N M, Chen Y Y, et al. Vicariance Biogeography Translation Corpus (in Chinese). Beijing: Encyclopedia of China Publishing House, 1996
- 6 Rieppel O. A case of dispersing chameleons. Nature, 2002, 415: 744-745
- 7 Raven P H, Axelrod D I. Angiosperm biogeography and past continental movements. Ann Missouri Bot Gard, 1974, 61: 539-673

- 8 Vogel S, History of the Malpighiaceae in the light of pollination ecology. Mem N Y Bot Gard, 1990, 55: 130-142
- 9 Doyle J A, Sauquet H, Scharaschin T, et al. Phylogeny, molecular and fossil dating, and biogeographic history of Annonaceae and Myristicaceae (Magnoliales). Int J Plant Sci, 2004, 165(suppl 4): s35-s67[DOI]
- 10 Crepet W, Nixon K, Gandolfo M A. Fossil evidence and phylogeny: The age of major angiosperm clades based on mesofossil and macrofossil evidence from Cretaceous deposits. Am J Bot, 2004, 91(10): 1666-1682
- 11 Sun G, Dilcher D L, Zheng S, et al. In search of the first flower: A Jurassic angiosperm, *Archaefructus*, from northeast China. Science, 1998, 282: 1692-1695[DOI]
- 12 Sun G, Ji Q, Dilcher D L, et al. Archaefructaceae, a new basal angiosperm family. Science, 2002, 296: 899–904[DOI]
- 13 Doly J A. Molecular, morphology, fossil, and the relationship of angiosperm and Gnetales. Mol Phylogent Evol, 1998, 9: 448-462[DOI]
- 14 Matthews S, Donoghue M J. The root of angiosperm phylogeny inferred from duplicate phytochrome genes, Science, 1999, 286: 947-950[DOI]
- 15 Crane P R, Blackmore S. Evolution, Systematics, and Fossil History of the Hamamelidae, Oxford: Clarendon Press, 1989. 1–353
- 16 Crepet W L, Nixon K C. The fossil history of stamens. In: D'Arcy W G, Keating R C, eds. The Anther: Form, Function and Phylogeny. Cambridge: Cambridge Univ Press, 1996. 25–57
- 17 Gandolfo M A, Nixon K C, Crepet W L, et al. Oldest known fossil flowers of monocotyledons. Nature, 1998, 394: 532-533[DOI]
- 18 Gandolfo M A, Nixon K C, Crepet W L. Monocotyledons: A review of their early Cretaceous record. In: Wilson K, Morrison D. eds. Proceedings of the Second International Conference on the Comparative Biology of the Monocotyledons. Sydney: CSIRO, 2000. 44-52
- 19 Zhou Z K, Crepet W L, Nixon K C. The earliest fossil evidence of the Hamamelidaceae: Late Cretaceous (Turonian) Inflorescences and fruits of Altingioideae. Am J Bot, 2001, 88(5): 753-766
- Nixon K C. Paleobotany in cladistics and cladistics in paleobotany: Enlightenment and uncertainty. Rev Paleobot Palynol, 1996, 90: 361-373[DOI]
- 21 Nixon K C. The parsimony ratchet, a new method for rapid parsimony analysis. Cladistics, 1999, 15: 407-414[DOI]
- 22 Crane P R, Friis E M, Pedersen K R. The origin and early diversification of angiosperms. Nature, 1995, 374: 27–33[DOI]
- 23 Davis C C, Bell C D, Mathews S, et al. Laurasian migration explains Gondwanan disjuntions: Evidence from Malpighiaceae. Proc Natl Acad Sci USA, 2002, 99(10): 6833-6837[DOI]
- 24 Magallón S, Sanderson M J. Absolute diversification rates in angiosperm clades. Evolution, 2001, 55: 1762–1780
- 25 Scotese C R. Earth history Volume 1: Paleogeography Paleomap.

Texas: Project ArLington, 2001. 52

- 26 Raxworthy C J, Forstner M R J, Nussbaum R A. Chameleon radiation by oceanic dispersal. Nature, 2002, 415: 784-787
- 27 Week A, Daly A W, Simpson B B. The Phylogenetic history and biogeography of the frankincense and myrrh family (Burseraceae) based on nuclear and chloroplast sequence data. Mol Phylogenet Evol, 2005, 35(1): 85-101[DOI]
- 28 Fritsch P W. Phylogeny and biogeography of the flowering plant genus *Styrax* (Styracaceae) based on chloroplast DNA restriction sites and DNA sequences of the internal transcribed spacer region. Mol Phylogenet Evol, 2001, 19(3): 387-408[DOI]
- 29 Gottschling M, Diane N, Hilger H H, et al. Testing hypothesis on disjunctions present in the primarily woody Boraginales: Ehretiaceae, Cordiaceae, and Heliotropiaceae, inferred from ITS, sequence data. Int J Plant Sci, 2004, 165(Suppl 4): s123 – s135[DOI]
- 30 Renner S S. Tropical trans-Atlantic disjunctions, sea surface currents, and wind patterns. Int J Plant Sci, 2004, 165(suppl 4): s23s33[DOI]
- 31 Nathan R. Long-distance dispersal research: Building a network of yellow brick roads. Diversity Distrib, 2005, 11(2): 125-130[DOI]
- 32 Nie Z L, Wen J, Sun H, et al. Monophyly of *Kelliogia* Torr Ex Benth (Rubiaceae) and evolution of its intercontinental disjunction between western North American and Eastern Asia. Am J Bot, 2005, 92(4): 642-652
- 33 Houle A. Floating islands: A mode of long-distance dispersal for small to medium-sized terrestrial vertebrates. Diversity Distrib, 1998, 4(5-6): 201-216
- 34 Houle A. The origin of platyrrhines: An evaluation of the antarctic scenario and the floating island model. Am J Phys Anthropol, 1999, 109(4): 541-559[DOI]
- 35 Darwin C R. On the Origin of Species by Means of Natural Selection, 11th ed. London: John Marry, 1991
- 36 Nathan R. The challenges of studying dispersal. Trends Ecol Evol, 2001, 16: 481-483[DOI]
- 37 Wu C Y, Lu A M, Tang Y C, et al. The Families and Genera of Angiosperms in China: A Comprehensive Analysis (in Chinese). Beijing: Science Press, 2003. 1–47
- 38 Wu C Y, Zhou Z K, Li D Z, et al. The areal-types of world families of seed plants. Act Bot Yunnan (in Chinese), 2003, 25(3): 245– 257
- 39 Zhou Z K. Origin, systematics and distribution of Cloranthaceae. Act Bot Yunnan (in Chinese), 1993, 15(4): 321-331
- 40 Anderson W R. The origin of the Malpighiaceae: the evidence from morphology. Mem N Y Bot Gard, 1990, 64: 210-224
- 41 Davis C C, Anderson W R, Donoghue M J. Phylogeny of Malpighiaceae: Evidence from chloroplast *ndhF* and *trnL-F* nucleotide sequences. Am J Bot, 2001, 88(10): 1830–1846
- 42 Cameron K M, Chase M W, Anderson W R, et al. Molecular sys-

tematics of Malpighiaceae: Evidence from plastid *rbc*L and *mat*K sequence. Am J Bot, 2001, 88(10): 1847–1862

- MacPhee R D E, Iturralde-Vinent M A. Origin of the Great Antillean land mammals, 1: New Tertiary fossils from Cuba and Puerto Rico. Am Mus Novitates, 1995, 3141: 1-31
- 44 Iturralde-Vinent M A, MacPhee R D E. Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. Bull Am Mus Nat Hist, 1999, 238: 1-95
- 45 Tiffney B H. The Eocene North Atlantic land bridge: Its importance in Tertiary and modern phytogeography of the Northern Hemisphere. J Arnold Arbor Harv Univ, 1985, 66: 243-273
- 46 Renner S S, Clausing G, Meyer K. Historical biogeography of Melastomataceae: The roles of Tertiary migration and long-distance dispersal. Am J Bot, 2001, 88(7): 1290-1300
- 47 Chanderbali A S, van der Werff H, Renner S S. Phylogeny and historical biogeography of Lauraceae: Evidence from the chloroplast and nuclear genomes. Ann Missouri Bot Gard, 2001, 88: 104–134
- 48 Klaver C J J, Bohme W. Phylogeny and classification of the Chameleonidae (Sauria) with special reference to hemipenis morphology. Bonn Zool Mon, 1986, 22: 1-64
- 49 Rieppel O, Crumley C. Paedomorphosis and skull structure in Malagasy chameleons (Reptilia: Chamaelondiae). J Zool Lond, 1997, 243: 351-380
- 50 Rieppel O. The phylogenetic relationships within the Chamaeleonidae, with comments on some aspects of cladistic analysis. Zool J Linn Soc, 1987, 89: 41-62
- 51 Vences M. Origin of Madagascar's extant fauna: A perspective from amphibians, reptiles and other non-flying vertebrates. Ital J Zool, 2004, 2(suppl): 217-228
- 52 McCall R A. Implications of recent geological investigations of the Mozambique Channel for the mammalian colonization of Madagascar. Proc Biol Sci, 1997, 264: 663-665[DOI]
- 53 Wallace A R. The Geographical Distribution of Animals. New York: Harper and Brothers, 1876
- 54 Higgins S I, Nathan R, Cain M L. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology, 2003, 84(8): 1945–1956
- 55 Higgins S I, Richardson D M. Predicting plant migration rates in a changing world: The role of long-distance dispersal. Am Nat, 1999, 153: 464-475[DOI]
- 56 Cain M L, Dumman H, Muir A. Seed dispersal and the Holocene migration of woodland herbs. Ecol Monogr, 1998, 68(3): 325-347
- 57 Wilkinson D M. Plant colonization: Are wind dispersed seeds really dispersed by birds at large spatial and temporal scales? J Biogeogr, 1997, 24: 61-65
- 58 Clark J S. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. Am Nat, 1998, 152: 204– 224[DOI]
- 59 Nathan R. Seeking the secrets of dispersal. Trends Ecol Evol, 2003,

8(6): 275-276[DOI]

- 60 Nathan R, Sapir N, Trakhtenbrot A, et al. Long-distance biological transport processes through the air: Can nature's complexity be unfolded *in silico*? Diver Distr, 2005, 11: 131-137[DOI]
- 61 Soons M B, Ozinga W A. How important is longdistance seed dispersal for regional survival of plant species? Diver Distr, 2005, 11: 165-172[DOI]
- 62 Kinlan B P, Gaines S D, Lester S E. Propagule dispersal and the scales of marine community process. Diver Distr, 2005, 11: 139– 148[DOI]
- 63 Gottschling M, Lilger H H, Wolf M, et al. Seondary structure of the ITS1 transcript and its application in a reconstruction of the phylogeny of Boraginales. Plant Biol, 2001, 3: 629-636[DOI]
- 64 Mouchaty S K, Catzeflis F, Janke A, et al. Molecular evidence of African Phiomorph-south American Caviomorpha clad and support for Hystricognathi based on the complete mitochondrial genome of the cane rat (*Thryonomys swinderianus*). Mol Phylogenet Evol, 2001, 18: 127-135[DOI]
- 65 Givnish T J, Millam K C, Evans T M, et al. Ancient vicariance or recent long-distance dispersal? Inferences about phylogeny and south American-African disjunction in Rapateaceae and Bromeliaceae based *anb*F sequence data. Int J Plant Sci, 2004, 165(suppl 4): s35-s54[DOI]
- 66 Renner S S, Meyer K. Melastomeae come full circle: Bio- geographic reconstruction and molecular clock dating. Evolution, 2001, 55: 1315-1324
- 67 Givnish T J, Evans T M, Zjhra M L, et al. Molecular evolution adaptive radiation, and geographica diversification in the amphiatlantic family Rapateaceae: Evidence from *ndh*F sequence data. Evolution, 2001, 54: 1915–1937
- 68 Higgins S I, Lavorel S. Revilla E Estimating plant migration rates under habitat loss and fragmentation. Oikos, 2003, 101: 354– 366[DOI]

- 69 Thorne R, Tropical plant disjunctions: A personal reflection. Int J Plant Sci, 2004, 165(suppl 4): s137-s138[DOI]
- 70 Chase M W, Stevenson D W, Wilkin P, et al. Monocot systematics: A combined analysis. In: Rudall P J, Cribb P J, Cutler D F, et al. eds. Monocotyledons: Systematics and Evolution. London: Royal Botanic Gardens, Kew, 1995. 685–703
- 71 Wu C Y. The areal-types of Chinese genera of seed plants. Acta Bot Yunnan (in Chinese), 1991, (Suppl 4): 1-6
- 72 Wang F, Li D Z, Yang J B. Molecular phylogeny of the Lardizabalaceae based on *trn*L-F sequence and combined Chloroplast data. Acta Bot Sin, 2002, 44(8): 971–977
- 73 Tiffney B H. Fruits and seeds of the Tertiary Brandon Lignite VII: Sargentodoxa (Sargentodoxaceae). Am J Bot, 1993, 80: 517−523
- 74 Manchester S R. Biogeographical relationships of North American Tertiary Xoras. Ann Missouri Bot Gard, 1999, 86: 472–522
- 75 Zhou Z K, Momohara A. Fossil history of some endemic seed plants of east Asia and its phytogeographical significance. Acta Bot Yannan, 2005, 27(5): 449-470
- Schuettpelz E, Hoot S R, Phylogeny and Biogeography of *Caltha* (Ranunculaceae) based on chloroplast and nuclear DNA sequences. Am J Bot, 2004, 91(2): 247-253
- 77 Doyle J A, Thomas A L. Phylogeny and geographic history Annonaceae. Geogr Phys Quatern, 1997, 51: 353-361
- 78 Fritsch P W, Phylogeny of *Styrax* based on morphological characters, with implications for biogeography and infrageneric classification. Syst Bot, 1999, 24: 356–378
- 79 Lavin M, Thulin M, Labat J N, et al. Africa, the odd man out: Molecular biogeography of Dalbergioid Legumes (Fabaceae) suggests otherwise. Syst Bot, 2000, 25: 449-467
- 80 Davis C C, Bell C D, Fritsch P W, et al. Phylogeny of Acridocarpus brachylophon (Malpighiaceae): Implications for tertiary tropical floras and Afro-asian biogeography. Evolution, 2002b, 56: 2395-2405