

Mitochondrial composition of and diffusion limiting factors of three social wasp genera *Polistes*, *Ropalidia*, and *Parapolybia* (Hymenoptera: Vespidae)

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Abstract

Background

Social wasps *Polistes*, *Ropalidia*, and *Parapolybia*, belonging to the subfamily Polistinae, have obviously different distribution patterns, yet the factors leading to this difference remain unknown.

Results

In this study, mitochondrial genomes (mitogenomes) of 21 species of these three wasp genera were used to phylogenetic analyses, including 17 newly sequenced ones. It is revealed that both evolutionary selection pressure of protein-coding genes (PCGs) and gene rearrangement events are related to the corresponding distribution patterns. In addition, our fossil-calibrated divergence time estimation suggests the diversification of *Polistes* was in the Late Cretaceous (~ 69 million years ago, Ma), and that of *Ropalidia* and *Parapolybia* occurred in the Tertiary (~ 61 Ma). In view of the divergence time and the history of continental drifts, we speculate that *Polistes* may spread from Africa to South America via the Atlantic Ocean rather than from Asia to South America. On the other hand, combining divergence time and climate changes of both past and the present-day, it is inferred that Quaternary Ice Ages and temperature could be limitation factors in their present distribution patterns.

Conclusions

There are obvious differences in the mitochondrial composition of *Polistes*, *Ropalidia*, and *Parapolybia* with different distribution ranges. According to the reconstructed time-calibrated framework, we found that the climate and the continental drifts are diffusion limiting factors of the three genera.

1. Background

The subfamily Polistinae (Hymenoptera: Vespidae), including more than 950 species of 26 genera and 4 tribes, are social wasps with wide distributions, playing a significant role in the community level and biological control [1–3]. Among the subfamily, *Polistes* Latreille, 1802 is a cosmopolitan and the largest genus with about 300 species [4, 5]. *Ropalidia* Guérin-Méneville, 1831, the third largest genus with more than 200 species, is distributed in a greater part of the Old World with a tropical or subtropical climate [6, 7]. *Parapolybia* de Saussure, 1854, including 13 species, is a small genus and with a much narrower distribution than *Ropalidia* [8]. Meanwhile, only these three genera in the subfamily Polistinae are distributed in China, also with obviously different distribution patterns that *Polistes* is widespread, whereas both *Ropalidia* and *Parapolybia* are mostly distributed to south of the Qinling Mountains–Huai River (QH) line (104°15'–120°21'E, 32°05'–34°18'N). Factors causing their difference of distributions in these three genera are still unknown.

There are many factors that influence the geographical distribution pattern of a species, such as the origin and evolutionary events, the movements of continental plates, the climate of species habitat, the vicissitudes of plant communities, and human activities [3, 9]. Combined with fossil evidence and distribution data of a species, phylogenetic analyses could infer the origin time, evolutionary history, ancestral distribution areas, and the formation history of the present distribution pattern of this species [10]. Mitochondrial genomes (mitogenomes) harbor characteristics of low levels of sequence recombination, short coalescent time, and generally rapid evolutionary rates in both vertebrates and invertebrates; therefore, phylogenetic trees constructed on mitogenomic sequences are always employed to solve the confusions in the origin time, evolutionary history, and distribution pattern [11, 12]. However, the phylogenetic analyses of *Polistes*, *Ropalidia*, and *Parapolybia* have never been studied using whole mitogenome data.

In this study, to explore the origin time of *Polistes*, *Ropalidia*, and *Parapolybia*, as well as to elucidate the factors that contribute to their present distribution patterns, mitogenomes of 17 species belonging to *Polistes*, *Parapolybia*, and *Ropalidia* were sequenced. The gene orders in mitogenomes of the three genera were systematically compared with that in the putative ancestral of Hymenoptera to find the structure and composition which might be related to the distribution patterns [13–15]. And these data, in combination with two previously reported mitogenomes of *Polisties* and one of *Parapolybia* [16–17], were used to reconstruct phylogenetic trees and estimate origin time. Furthermore, based on the origin time and current distributions, it was analyzed that the vicissitudes of both continental plates and global climates might influence the diversities and distribution patterns of these genera.

On the other hand, the early classifications of both *Ropalidia* and *Parapolybia* have undergone relatively extensive transfers as follows, respectively. *Ropalidia* Guérin-Ménéville, 1831 was classified to Ropalidiinae and *Parapolybia* to Epiponinae [18]. Then, Richards classified *Ropalidia* to Ropallidiini and *Parapolybia* to Polybiidae [19]. Li classified *Polistes*, *Ropalidia*, and *Parapolybia* to different families, namely Polistidae, Ropalidiidae, and Polybiidae, respectively [20]. Hereafter, Carpenter divided Polistinae into four tribes in the light of morphology: Epiponini, Mischocyttarini, Polistini, and Ropalidiini; both *Parapolybia* and *Ropalidia* belonged to the tribe Ropalidiini, and *Polistes* to Polistini [4, 21]. Subsequently, the phylogeny of Polistinae using morphological and behavioral characteristics, as well as partial mitogenomic sequences and nuclear markers (*CO1*, *12S*, *16S*, *28S*, *H3*, and *EF1- α*) was investigated, the result of which supported that Polistinae consisted of four tribes [22]. As long as sequence data are available, there has been constant debates about which data can yield the most accurate result when the topologies obtained from different data sets conflict [23]. Whereas, the mass applications of whole mitogenome data provide great potential for resolving the phylogeny and biogeography which cannot be solved by one or two mitogenomic sequences or nuclear markers [24]. By the way, the classifications of *Polistes*, *Ropalidia*, and *Parapolybia* were further clarified with the application of whole mitogenome data in this study.

2. Materials And Methods

2.1 Sample collection and DNA extraction

A total of 17 species of these three genera were selected for whole mitogenome sequencing (Table. S1). All the specimens were stored in 95% ethanol prior at -20°C in Chongqing Normal University (CQNU). Total DNA was extracted from the muscle tissues of thorax using the DNeasy DNA Extraction kit (QIAGEN Shanghai, China). The concentration of double-stranded DNA (dsDNA) in extraction was assayed on a Qubit fluorometer using a dsDNA high-sensitivity kit (Invitrogen Shanghai, China).

2.2 Sequence assembling and analyses

The genomic DNA from each sample was pooled and quantified to be 5.0 µg, and the Illumina TruSeq library was constructed from these DNA, of which the average size of inserted fragment was 480 bp. The library was sequenced on the Illumina Hiseq 2500 platform at Berry Genomics, Beijing; 6 Gb clean data was obtained for each species. These reads were used in *de novo* assembly with IDBA-UD after getting rid of adapters, unpaired, and lower quality reads [25]. The parameters used for assemblies with IDBA-UD were a similarity threshold of 98% and minimum and maximum K values of 80 and 240 bp. Using primers designed by Simon [26], the *COX1* and *srRNA* used as targeting sequences were amplified by standard PCR reactions, which were used to confirm if the mitogenomes was assembled from the pooled sequencing files. The BLASTn search was used to identify the mitogenomes sequences based on the reference of bait sequences [27].

PCGs, tRNAs, rRNAs, and control regions were identified by searching homologous sequences against the publicly available Vespidae mitogenomes using ClustalX 1.8 [28]. Nucleotide composition was calculated by using MEGA 6.0 [29]. CG View was used to circularize the mitogenomic sequences [30]. The software package DnaSP 5.0 [31] was used to calculate the non-synonymous (K_a) and synonymous (K_s) substitution ratio (K_a/K_s) for each sequenced mitogenome. To test significance of K_a/K_s and A+T content among *Polistes*, *Ropalidia*, and *Parapolybia*, the one-way analysis of variance (ANOVA) was used as implemented in R core packages with default settings [32]. Gene rearrangement histories of these three wasp genera were reconstructed by using TreeREx 1.85 [33].

2.3 Phylogenetic analyses

In the phylogenetic analyses, 17 whole mitogenome sequences generated in this study and 18 from previous researches were included, representing the four subfamilies of Vespidae (Table. S2). The mitogenomic sequences of *Apis cerana* (Apidae), *Megachile sculpturalis* (Megachilidae), and *Philanthus triangulum* (Crabronidae) were used as outgroups. Multiple alignments were aligned individually by codon-optimized using the L-INS-i strategy with MAFFT algorithm [34], and ambiguous alignment regions were trimmed from the sequences using Gblocks program in TranslatorX [35, 36]. Alignments of individual genes were concatenated as two datasets: 1) PCGR: 13 PCGs and 2 rRNA; 2) AA: amino acid sequences of the 13 PCGs. The two datasets were used in our phylogenetic analyses. The Bayesian inference (BI) with MrBayes v3.1.2 [37] was performed for phylogenetic inference. The BI tree was constructed with the average deviation of split frequencies below 0.01, approximately 1,000,000

generations were conducted for the matrix, and each set was sampled every 1,000 generations with a burn-in of 25%. Maximum likelihood (ML) analysis was performed by PHYML [38] online web server with default parameters and the node support values were evaluated via a bootstrap test with 100 replicates.

2.4 Divergence time estimation

The divergence time was estimated using BEAST v.2.5.0 [39]. The GTR + I + G nucleotide substitution model and the speciation Yule model were selected as the tree priors with the uncorrelated lognormal relaxed molecular clock model. Two independent Markov Chain Monte Carlo (MCMC) runs, each had a chain length of 1,000,000 generations with sampling every 1,000 generations and a first 25% burn-in, were performed to estimate the divergence time. *Paleovespa menatensis* of Vespinae (64 – 60 million years ago, Ma) and *Symmorphus senex* of Eumeninae (94 – 90 Ma) were selected for calibration [40, 41].

3. Results

3.1 The latest distributions of the three genera

The distributions of the three genera based on the latest statistics of species checklists [4, 5, 7, 42–53] were newly sorted out and located on the world map using Bigemap (<http://www.bigemap.com>) (Fig. 1). The northernmost distributions of *Polistes*, *Ropalidia*, and *Parapolybia* are Victoria of Canada (123°22' W, 48°25' N), Pakistan (71°27' E, 29°79' N), and Turkey (39°46' E, 34°27' N), respectively. While the southernmost distributions of these three genera are Río Negro of South Africa (63°03' W, 40°82' S), Western Cape of South Africa (19°82' E, 33°37' S), and Timor Island (124°05' E, 9°62' S), respectively.

3.2 Mitogenomic composition of the three genera

In this study, for the first time, 17 whole mitogenome sequencing on *Polistes*, *Ropalidia*, and *Parapolybia* was performed, which greatly enriches the mitogenome data of Vespidae. Most newly sequenced mitogenomes contain 37 genes (Fig. S1), including 13 PCGs, 22 tRNA genes, and two rRNA genes, as well as a control region, which has been conformed in most metazoan animals [54]. However, several mitogenomes are short of one or two genes. For example, *Ropalidoa* sp. lacks *trnY*; *Ro. magnanima* lacks *trnQ* (Fig. S2). Among these three genera, the A + T content of *Polistes* is the highest, and the GC-skew and AT-skew are considerably variable in *Ropalidia* (Fig. S3). Their nucleotide composition is significantly biased toward adenine and thymine, with an A + T content more than 80% and the order of their A + T content is *Polistes* > *Ropalidia* > *Parapolybia*. And the result of ANOVA suggests that there is a significant difference ($P = 0.0020$) among the A + T content of the three wasp genera (Fig. 2b). Hua et al. suggested that the variations of GC-skew and AT-skew are related to species biodiversity of geographical distributions with different widths [55]. The most widely distributed genus is *Polistes* among the three; however, it does not show the most significant variation in GC-skew or AT-skew, which may be due to the fact that these three genera have undergone different adaptation or selection processes.

The results of *Ka/Ks* values of the three genera for 13 PCGs indicate that the order of *Ka/Ks* values is *Polistes* > *Ropalidia* > *Parapolybia* for all PCGs but *ND6*, *COX2* and *CYTB* (Fig. 2a). Meanwhile, the average *Ka/Ks* value of total PCGs in *Polistes* is the highest among the three wasp genera and that of *Parapolybia* is the lowest. Significant difference ($P = 0.0023$) were observed among the *Ka/Ks* values of the three wasp genera (Fig. 2c). It has been reported that the duration and magnitude of *Ka/Ks* elevation depend on the effective population size [56]. Considering the fact that the distribution of *Polistes* is the widest while that of *Parapolybia* is the narrowest, we speculate that the selective pressure on these three genera may be related to species biodiversity of geographical distributions with different widths.

3.3 Gene arrangements

Mitogenomes of insects are usually stable in structure; gene orders are relatively conservative, and recombination events rarely occur in the evolutionary history of insects [57]. However, the number of mitochondrial gene rearrangements in the Hymenopteran lineages was clearly toward an increase [58]. Our results indicate that at least six gene rearrangement events occurred. As shown in Fig. 3, the arrangements of 13 PCGs and 2 rRNA genes in mitogenomes of the three genera are identical to that of the putative ancestral Hymenoptera. A gene rearrangement event is common in *Ropalidia* and *Parapolybia* mitogenomes, that is, the translocation of *trnY* from the location between *trnC* and *cox1* to the upstream of *trnI* (T1); the recombination events seem to be the most plausible explanation for this translocation. In addition, the swap of positions between *nad1* and *trnL1* resulted in a rearranged gene order of *trnS2-trnL1-nad1* in *Parapolybia* mitogenomes, which is also found in *Polistes* and can be explained by tandem-duplication-random-loss (TDRL) models (TDRL II and TDRL III). Furthermore, it was also identified that intergenic spacers (IGSs) between *trnS2* and *trnL1*, and between *nad1* and *rnl* in both *Parapolybia* and *Polistes*, corresponded to random gene losses, providing evidence supporting gene duplication and deletion events in gene rearrangements (TDRL II and TDRL III). However, in *Ropalidia*, the swap of positions between *trnS2* and *trnL1* led to a rearranged gene order of *trnL1-nad1-trnS* (TDRL I) and there are also two IGSs between *trnS2* and *cytb*, and between *nad1* and *rnl*. Moreover, three more rearrangement events were found in *Polistes*: *trnD* from the downstream of *trnK* to its upstream in *Po. jokahamae* (TDRL IV); *trnQ* from the downstream of *trnI* to its upstream in *Po. snelleni*, *Po. sagittarius*, and *Po. rothneyi iwatai*; *trnY* translocated from the location between *trnC* and *cox1* to the upstream of *trnI* (T2) in six sequenced species. The IGSs between *trnQ* and *trnY*, *trnY* and *trnI*, and *trnI* and *trnM* in *Po. snelleni*, *Po. Sagittarius*, and *Po. rothneyi iwatai* corresponded to random gene losses and genes separated by the translocation of *trnY*, providing evidences that support gene duplication, deletion, and recombination events in gene rearrangements (Fig. S4). Our results indicate that more than three rearrangement events occurred in *Polistes* and two in *Ropalidia* and *Parapolybia*, which might be explained by the fact that the wider the species geographical distribution is the richer the environment diversity is. This further resulted in an increase in the selective pressure, which might lead to the occurrence of gene rearrangements.

3.4 Phylogenetic relationships and divergence time estimation

In this study, the PCGR and AA datasets were used to individually reconstruct phylogeny of *Polistes*, *Parapolybia*, and *Ropalidia*. Using both BI and ML methods, four phylogenetic trees were generated, and no significant difference was observed in either BI or ML tree between the two datasets. The monophyly of each genus is well supported in all trees with bootstrap values greater than 80 and posterior probabilities of at least 0.89 (Fig. S5). In Vespidae, the phylogenetic relationship Stenogastrinae + (Eumeninae + (Vespinae + Polistinae)) is supported by transcriptomic and other molecular studies [59]. Polistinae forms a sister relationship with Vespinae, which is supported by previous studies on both morphological characteristics and molecular data [22, 60, 61]. In addition, within the subfamily Polistinae, the relationship (*Ropalidia* + *Parapolybia*) is concordant with previous morphological analysis of Polistinae that the two genera belong to one tribe [4, 21].

Given that the topology of phylogenetic trees between the two datasets was similar, the PCGR dataset was used to estimate divergence time as it had higher node support values in initial phylogenetic assessment. The result (Fig. 4) indicates that the subfamily Polistinae evolved over a period of 75 Ma, which is consistent with an earlier report [62]. Meanwhile the genus *Polistes* diverged at around 69 Ma, *Parapolybia* + *Ropalidia* were separated from the subfamily Polistinae at around 61 Ma, and the origin of *Parapolybia* was later than *Ropalidia*.

4. Discussion

4.1 Effects of continental drifts on the three genera

It is generally recognized that continental drifts play a key role in the origin and evolution of organisms [63]. There is a hypothesis that the subfamily Polistinae probably diverged from other Vespidae at the breakup of Gondwanaland (~ 135 Ma) and their Gondwanian connections were via tropical Africa and tropical South America [22]. However, the divergence time of Polistinae estimated based on whole mitogenome data in this study (75 Ma) is greatly later than the breakup of Gondwanaland, approximately 60 million years (Myr) after the fragmentation of Gondwana. The early notion generally was that *Polistes* first evolved in the Oriental tropics, whence it dispersed to the rest of the globe, with an invasion of the New World occurring via Beringia [64]. Whereas, some later phylogenetic studies have suggested that *Polistes* dispersed into the New World from the Old World, and South America was recovered as the ancestral area for all *Polistes* in the New World [22, 65]. In the view of how *Polistes* dispersed from the Old World to the New World, the two aforementioned hypotheses are inconsistent (Fig. 5). In our present study, by tracing the history of plate drifts, it was found that at the estimated origin time of *Polistes* (~ 69 Ma), North America had been separated from Laurasia during the Jurassic (208 – 135 Ma). Even though a narrow land channel was formed through the Bering Strait due to the influence of glaciers in the Pleistocene (~ 1.0 Ma), the climate in the Pleistocene period was extremely cold that the exchange of species was heavily prevented between Europe and North America [66]. Meanwhile, at the time *Polistes* originated, the tropical Gondwana had been broken for 40 Myr, and there were no existing uninterrupted land bridges between tropical Africa and South America after 80 Ma. Given the fact that the prior

existence of land connections cannot explain the present distribution of *Polistes*, the mismatch between the divergence time of *Polistes* and tectonic fragmentation implies an oceanic dispersal.

The oceanic dispersal of *Polistes* from the Old World to South America may occur in two routes: trans-Atlantic Ocean between South America and Africa, and trans-Pacific Ocean between Asia and South America. We compared the possibilities of these two routes. Up to date, South America is separated from Africa by at least 2,600 km of ocean, and the Atlantic Ocean first appeared well after the onset of the Gondwana breakup (~ 110 Ma) [67]. According to rates of motion of the South Atlantic Ocean (22–28 mm/a) based on International Terrestrial Reference Frame 2000 (ITRF2000) [68], we determined that the distance between South America and Africa at 69 Ma was 902–1,148 km, which is consistent with that of Sclater [69]. The study of Ford et al. indicated the shortest distance between Africa and South America was around 1,000 km in a straight line (from present-day Sierra Leone to Paraíba state, in Brazil) at 50 Ma, which also supports our estimated distance [70]. Correspondingly, South America is separated from Asia by at least 20,000 km of ocean [71]. The Pacific Ocean evolved from Panthalassa in the Late Carboniferous (314 – 290 Ma), and it had been shrinking owing to the fragmentation of Gondwana, and the expansion of the Indian Ocean and Atlantic Ocean [72], which means South America was separated from Asia by more than 20,000 km of ocean at 69 Ma. Hence, it is easier to understand (more acceptable) that the *Polistes* may spread to South America via the Atlantic Ocean due to the significantly smaller distance.

On the other hand, trans-ocean migrations may also rely on the presence of volcanic islands and rafting on buoyant vegetation. In the Atlantic Ocean, several islands of considerable size (more than 200 km in length) persisted along the present-day submerged Rio Grande Rise and Walvis Ridge at 50 Ma and the long set of islands (at least 800 km in length) had stretched from the Brazilian coast at 20° S (at the present-day Martin Van Archipelago) at 50 – 40 Ma [73]. Likewise, there were also many islands in the Pacific Ocean such as Fijian Islands, Borneo, West Sulawesi, and Hawaii Islands, formed by volcanic eruptions in the Late Cretaceous (100 – 65 Ma) [74]. Among these islands, the closest one to South America called Adamstown was more than 6,000 km away, a distance much longer than that between South America and Africa at 69 Ma [75]. Furthermore, animals had more difficulties in crossing ocean barriers than plants, and many animals attached to rafting on buoyant vegetation to trans-ocean [76]. Therefore, the shorter distance between South America and Africa during the origin of *Polistes* inspired us to think whether *Polistes* originated in Asia or Africa—the *Polistes* species may disperse from Africa to South America via the volcanic islands and/or rafting on buoyant vegetation, and finally to North America via the Isthmus of Panama between South and North America.

Ropalidia and *Parapolybia* are distributed in the Old World, and their divergence time is estimated at 61 Ma in the Palaeocene (65 – 53 Ma). During this period, Africa collided with Europe, leading to the formation of Alps. In addition, even though Indian and Oceania were separated from the Gondwanaland during the Late Jurassic (~ 135 Ma), Indian also collided with Asia in Southern Tibet in the Eocene (53–36.5 Ma). Hereafter, all the continents of the Old World except Australia had been connected until the present day [63]. According to the formation history of the Old World, there should be chances that

Ropalidia and *Parapolybia* spread among various plates except Australia. There were many islands, such as Philippine Islands and New Guinea, between Australia and the Eurasian subcontinent at 65 – 53 Ma [66], it is possible that the two genera *Ropalidia* and *Parapolybia* spread to Australia through these islands. Our inference is also supported by the result of Saito et al. that the current faunal composition and distribution pattern of *Ropalidia* in Australia actually originated in New Guinean and migrated via the Cape York Peninsula and further speciated in Australia [77]. In this study, the questions that where *Ropalidia* and *Parapolybia* originated and why *Parapolybia* species are not recorded in Australia remain unanswered, which require further information.

4.2 Effects of climate changes on the three genera

Climate changes also have major impacts on terrestrial biodiversity, directly affecting species distribution patterns [78, 79]. In our study, the last major climate change is traced back to the start of Quaternary Ice Ages (2.6-0.015 Ma) [80], because the current entire northern fauna and flora had been greatly changed during Quaternary Ice Ages when the European ice sheets covered the lands in Europe including Siberia to Mongolia, and the North American ice sheets moved from Canada to the northern United States, where it was extreme cold that many animals and plants had to move to the south [80, 81]. And the current climate had not been formed until the end of the Pleistocene (~ 0.015 Ma) [80, 82]. The last Ice Age ended at the beginning of the Holocene (0.015 Ma), and then the climate in the Holocene (0.015 Ma-present) became warmer, which was similar to the present-day climate [83]. As the climate getting warmer, some animals and plants migrated backward to the north [84]. Currently, there are a few of *Polistes* and few of both *Ropalidia* and *Parapolybia* distributed in the areas covered by ice sheets during Quaternary Ice Ages. Therefore, it may be inferred that Quaternary Ice Ages was a limitation factor in the northernmost distributions of the three genera.

Furthermore, it has been indicated that temperatures are important in defining the scope for intrasexual signaling in social wasps and play a role in maintaining variations in intrasexual traits in the view of sexual selection [85]. The most suitable temperature for social wasps is 25°C and the most comfortable relative humidity is 50–70% [86, 87]. The average annual climate in Antarctica is -25°C and the highest temperature in the North Pole area is -8°C [88], which may be one of the reasons that the wasps are not distributed there. There is a long winter and short summer in the middle temperate zone (40° N to 50° N, 40° S to 50° S) [89], including Mongolia Plateau, most of Northeast China, and North Canada, where annual temperatures vary greatly and the living animals are mostly homoiothermic animals [90]. In view of the influence of the temperature, most of wasps have the habit of overwintering [89], and long-term exposure to low temperatures would result in failure of wasps to overwinter [90], so there are relatively fewer *Polistes* and neither of *Ropalidia* and *Parapolybia* distributed in the middle temperate zone. To the contrary, in the subtropics (23°26' N to 40° N, 23°26' S to 40° S) and tropics (23°26' S to 23°26' N) [91], there is a small difference among the annual temperatures (above zero in winter), and plentiful precipitation and vegetation can support sufficient foods [92, 93]. Therefore, modern climate pattern also plays an important role in these genera distributions, as most of these wasps are coincidentally distributed in tropical and subtropical zones.

Meanwhile, the fact that *Polistes*, *Ropalidia*, and *Parapolybia* are abundant to the south of QH line in China can also be explained by our finding that the climate pattern influences species distributions. QH line is situated across the middle temperate, tropical and subtropical zones and is the north-south geographical, climatic, and demographic watershed of China. And it also serves as the boundary of the middle temperate and subtropical zones, and the boundary of the Palearctic and Oriental regions [94].

5. Conclusions

According to the mitogenomic composition of the three genera of *Polistes*, *Ropalidia* and *Parapolybia*, the variation in GC-skew or AT-skew is not positively corrected with geographical distributions, yet the Ka/Ks value shows the positive relationship with distribution range. In addition, gene rearrangement events are common in the three genera, and the more the number of the genus species is and the wider its geographical distribution is, the higher the probability of gene rearrangement occurrence is. In summary, variations of their mitogenomes may be accompanied by differences of the geographic distributions.

The monophyly of the genus *Polistes* is consistently supported with bootstrap values (BS) 100 and posterior probabilities (PP) 1, and a monophyletic Ropalidiini: (*Ropalidia* + *Parapolybia*) is concordant with previous morphological analysis of Polistinae. And then the divergence times demonstrate *Polistes* (at around 69 Ma) was diverged earlier than *Ropalidia* and *Parapolybia* (at around 61 Ma). Combining the history of continental drifts and their divergence time, continental drift is inferred to be one limiting factor in the current distributions of these three wasps. Hereafter, it is a more likely scenario that *Polistes* spread from the Old World to the New World by the transatlantic diffusion route rather than the hypothetical transpacific one. Meanwhile, *Polistes* and *Ropalidia* are considered to spread from Southeast Asia to Australia through New Guinea and other islands. Referring to the coverage of the ice sheet during Quaternary Ice Ages, we deduce that Quaternary Ice Ages is another limitation factor, especially which restricted the northernmost distributions of these three genera. Of course, it is confirmed that modern climate pattern plays a decisive role in the current distributions of these genera. Other potential factors such as human activities, plant communities and so on are needed to further explore.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Data accessibility: Mitochondrial genome sequences are accessible on GenBank and accession numbers were in electronic supplementary material of table S2.

Authors' contributions: Li Luo completed all the analysis and wrote the manuscript. Fossil-calibrated divergence estimation was generated with the help of Pan Huang. Bin Chen gave important comments on both this study and manuscript. Tingjing Li is responsible for the implementation of the entire project. All authors approved the final version of the manuscript and agree to be accountable for all aspects of the work.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Supplementary Material

Table. S1 Collection information of seventeen newly sequenced specimens.

Table. S2 The information of mitochondrial genomes in this study.

Fig. S1 Mitochondrial genomes of *Polistes*, *Ropalidia* and *Parapolybia* sequenced in this study. (In consideration of the almost consistent mitochondrial structure within genus, one inner circle of each genus was only presented in this paper.)

Fig. S2 Mtgenome organization of *Polistes*, *Parapolybia* and *Ropalidia* referenced with the ancestral insect mtgenomes. The underlined symbols are located on the N-strand and others on the J-strand. The yellow, blue and green blocks denote tRNAs, PCGs and control regions, respectively. The red font means rearranged genes.

Fig. S3 The A+T content (%), AT-skew, G+C content (%) and GC-skew of the *Polistes*, *Ropalidia* and *Parapolybia* whole mitogenomes.

Fig. S4 Mitochondrial gene rearrangements in *Polistes*, *Parapolybia* and *Ropalidia*. Genes are transcribed from left to right except those underlined, which have the opposite transcriptional orientation. The yellow, blue, purple and gray blocks denote tRNAs, PCGs, IGS and Random loss gene, respectively. IGS for the intergenic spacer.

Fig. S5 Reconstruction of phylogenetic tree determined by Bayesian inference and Maximum Likelihood methods based on PCGR and AA datasets of Vespidae mtgenomes. Bayesian posterior probabilities (left) and Parsimony bootstrap (right) are shown at relevant branches of the ML tree.

Figures

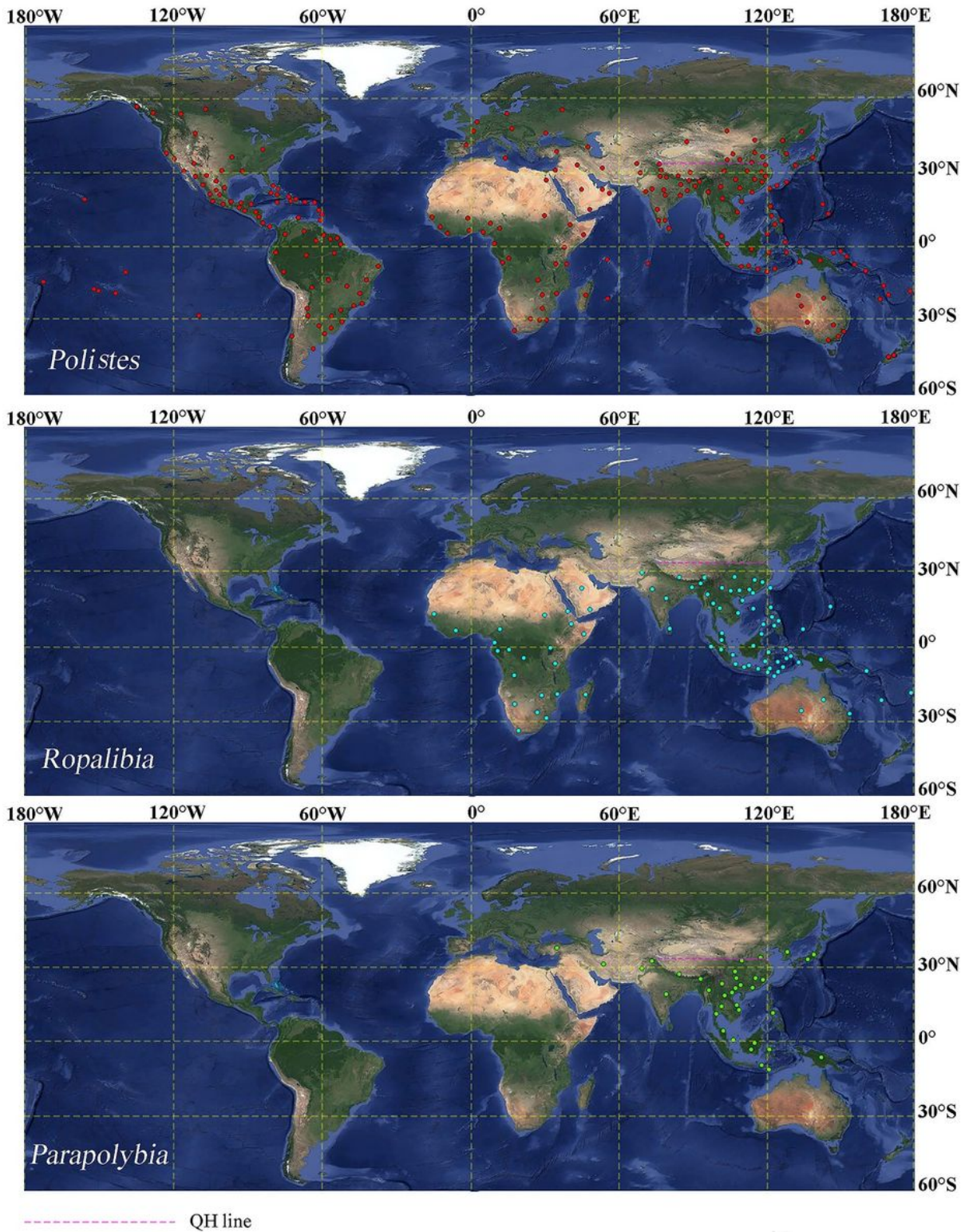


Figure 1

Distributions of *Polistes*, *Ropalidia*, and *Parapolybia*. The purple dashed line represents Qinling Mountains–Huai River (QH) line, and the dots in red, blue, and green represent the recorded distribution locations of *Polistes*, *Ropalidia*, and *Parapolybia*, respectively. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its

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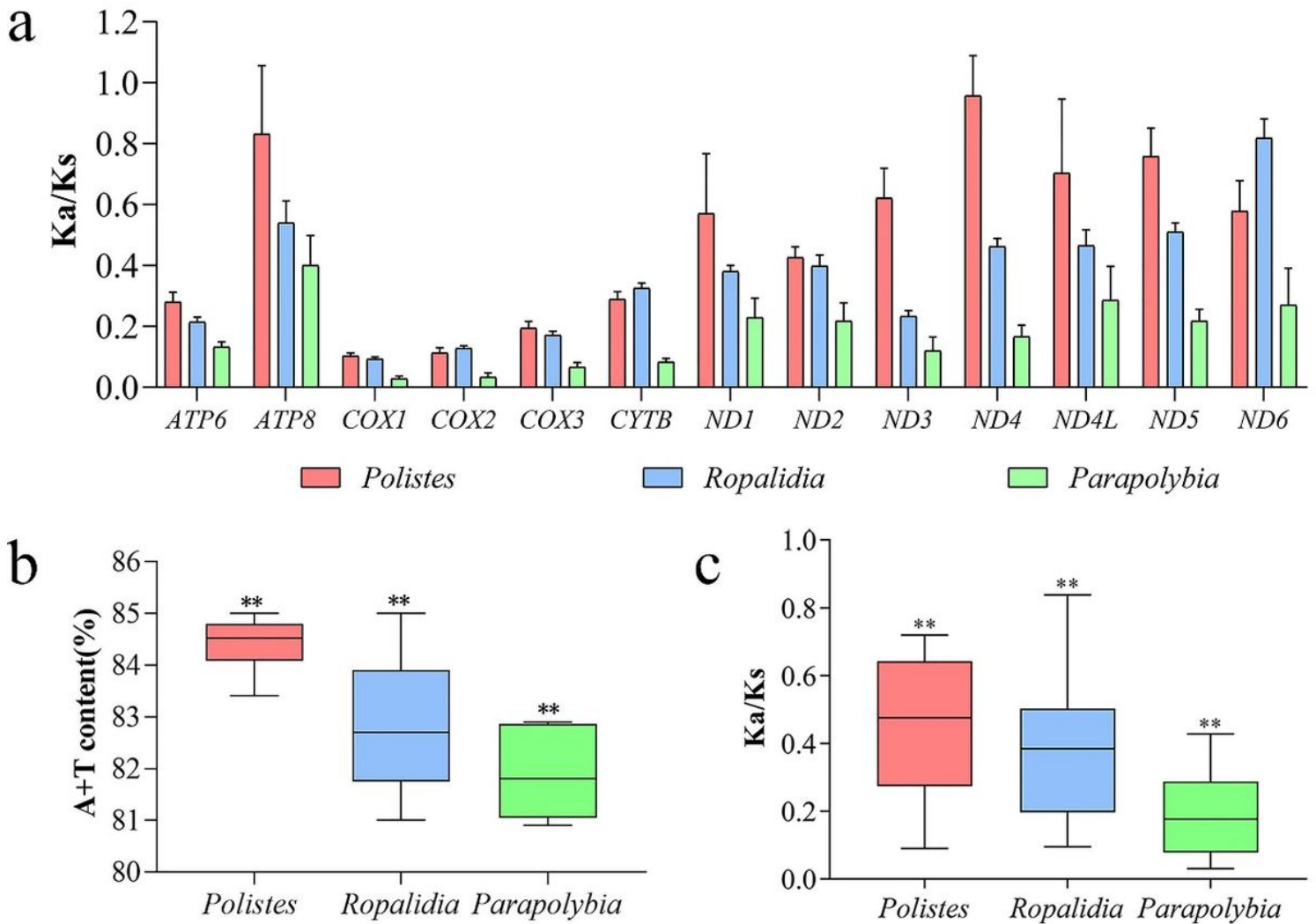


Figure 2

a: The Ka/Ks values of *Polistes*, *Ropalidia* and *Parapolybia* for 13 PCGs, respectively; b: The A+T content (%) of *Polistes*, *Ropalidia* and *Parapolybia* with whole mitogenomes, **: $P < 0.01$; c: The Ka/Ks values of *Polistes*, *Ropalidia* and *Parapolybia* for total PCGs, **: $P < 0.01$.

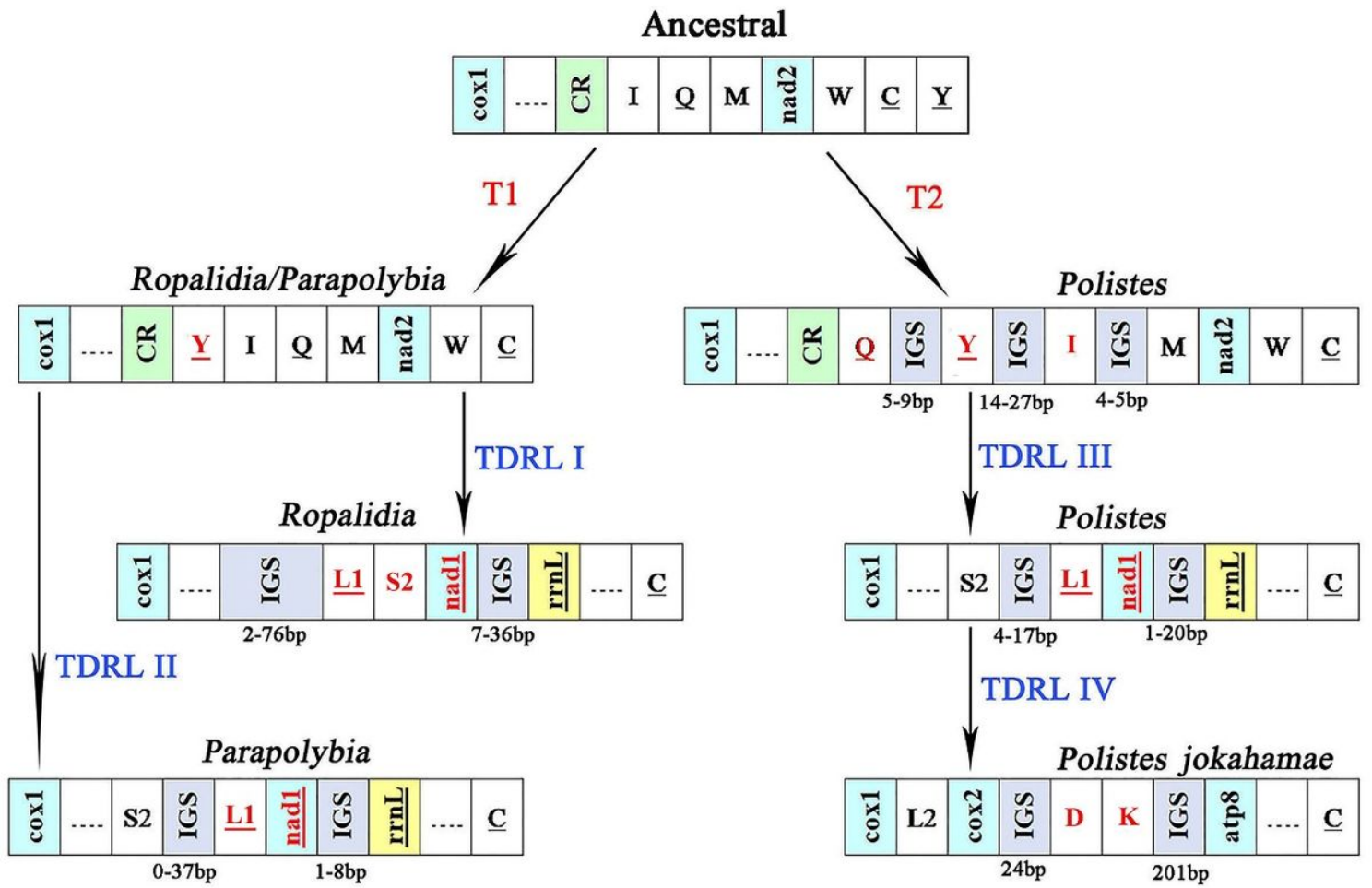


Figure 3

Mitochondrial gene rearrangements in *Polistes*, *Parapolybia* and *Ropalidia*. IGS for the intergenic spacer, TDRL for tandem-duplication-random-loss, T for translocation.

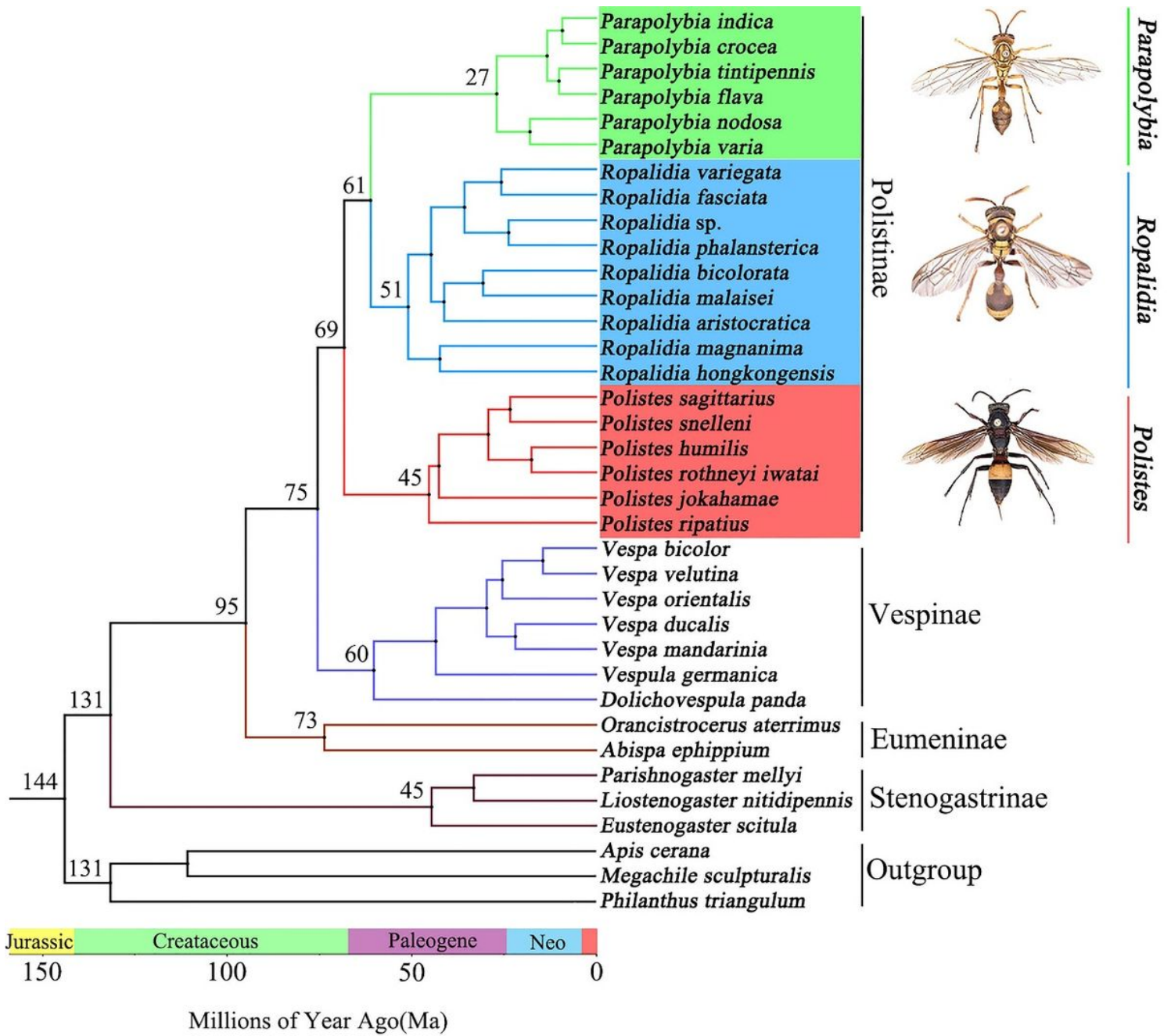


Figure 4

Evolutionary timescale for *Polistes*, *Parapolybia* and *Ropalidia* inferred from PCGR dataset.

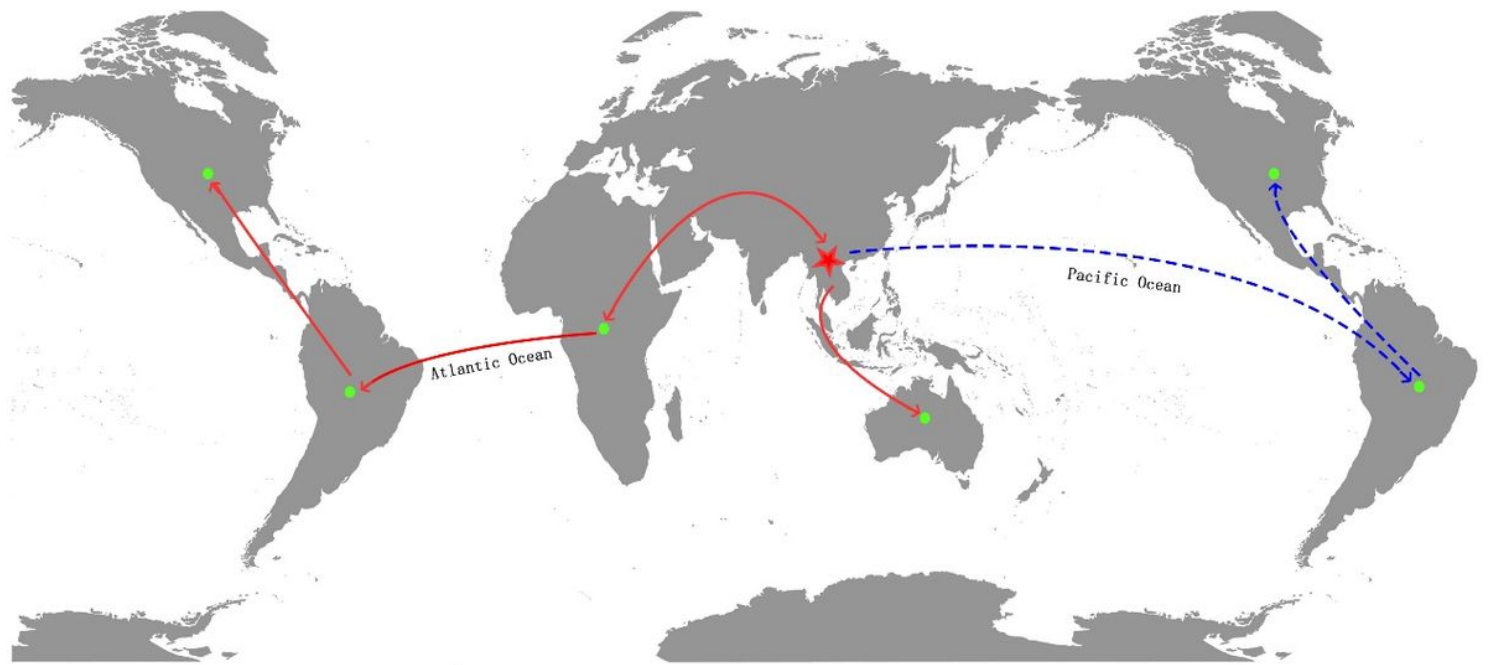


Figure 5

The proliferation route of *Polistes* from the Old World to the New World. Southeast Asia as the ancestor region of *Polistes* in New World is marked by a star. Transatlantic routes of invasion are shown in solid red line, potential transpacific routes of invasion are shown in blue dashes. The green dot only represents its continent rather than any specific location. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

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