Journal of Biogeography (*J. Biogeogr.*) (2008) **35**, 1241–1249

ORIGINAL ARTICLE

Biogeographical patterns of Chinese spiders (Arachnida: Araneae) based on a parsimony analysis of endemicity

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ABSTRACT

Aim The distributions of Chinese spiders are used to form biotic regions and to infer biogeographical patterns.

Location China.

Methods China was initially divided into 294 quadrats of 2° latitude by 2° longitude. The distributions of 958 species of spiders were summarized for each quadrat. Subsequently, these quadrats were pooled into 28 areas based on topographical characteristics and to a lesser extent on the distributions of spiders. Parsimony analysis of endemicity (PAE) was used to classify the 28 areas based on the shared distributional patterns of spiders.

Results China was found to have seven major biogeographical regions based on the distributional patterns of spiders: Western Northern region (clade B_2: Tibetan Plateau and Inner Mongolia-Xinjiang subregions), Central Northern region (clade B_3), Eastern Northern region (clade B_4), Central region (clade C_2), Eastern Southern region (clade C_3), Western Southern region (clade C_4), and Central Southern region (clade C_5).

Main conclusions The distributional patterns of Chinese spiders correspond broadly to geological provinces. A comparison of the geological provinces and the distributional patterns of spiders reveals that the spiders occur south of the geological provinces. Furthermore, a general biogeographical classification with five natural areas is suggested as follows: Tibetan Plateau, Central Northern, Eastern Northern, Western Northern (excluding Tibetan Plateau), and Southern regions.

Keywords
Biogeographical realm, biogeography, China, distributional patterns, geological provinces, Oriental realm, Palaearctic realm, PAE.

INTRODUCTION

Historical biogeography plays an important role in deciphering the evolution of biodiversity as well as in revealing the geological history of the Earth. The patterns and processes of biotic distribution are essential elements in the reconstruction of this history. From a biogeographical perspective, plate tectonics continually changes the surface of the Earth by keeping continents and ocean basins in constant motion. Continental movements, together with the rise and fall of sea levels, radically alter the configuration of land and sea, giving rise to vicariant events that isolate species of terrestrial plants and animals within specific regions (Scotese, 2004).

Although China lies in south-eastern Eurasia, it has a relatively independent geological history. Six primary plates are involved in its tectonic history, namely the North China, Tarim, Yangtze, Cathaysian plates, and parts of the Siberia and Gondwana plates. By the Pleistocene, seven collisions and integrations of these plates had united the ancient Siberian and European plates (Hsü & Chen, 1999; Wan, 2003). With approximately 200 tectonic-facies (Hsü & Chen, 1999), China has a complex topography, including towering mountains, basins of various sizes, undulating plateaus and hills, and fertile plains. Mountains occur as north-south terraced terrain with slopes that descend to the east and west. The highest terrace, the Qinghai-Tibetan Plateau – the 'roof of the world' – has an

doi:10.1111/j.1365-2699.2007.01843.x

average elevation of over 4000 m. The second highest terrace consists of Inner Mongolia, the Loess Plateau, the Yunnan-Guizhou Plateau, and the Tarim, Junggar and Sichuan basins. It averages 1000–2000 m in elevation. The third terrace, with an elevation of 500–1000 m, involves the Da Xingan, Taihang, Wushan, and Xuefeng mountains on the eastern coast of China. Sub-littoral areas on the Chinese continental shelf comprise the fourth terrace; the average depth of water is less than 200 m.

Geological complexity and history usually have a profound influence on the distributions of living organisms, and China is no exception to this rule. The complex topography and historical processes make the biogeographical study of the Chinese biota both intriguing and challenging.

Traditionally, China has been divided into two realms and seven biological provinces. The Palaearctic realm includes the North-eastern, Northern, Inner Mongolia-Xinjiang, and Qinghai-Tibetan biological provinces. The Oriental realm includes the South-western, Central, and Southern biological provinces. This division, originally established by Cheng & Zhang (1959), was later modified by Zhang & Zhao (1978) and Zhang (1998, 2004). To a great extent, this biogeographical classification was based on the distributions of vertebrates, primarily mammals and birds. Recently, MacKinnon *et al.* (1996) provided an empirical evaluation of the biogeographical patterns, and Xie *et al.* (2004) clustered overall similarity coefficients. Although these papers make significant contributions, the biogeographical patterns of other speciose taxonomic groups, such as arthropods, have been poorly assessed.

Unique in producing and using silk, spiders constitute the seventh largest order of animals (Coddington & Levi, 1991). They occur in almost every habitat, from marine intertidal zones to tundra and rocky peaks. Most spiders have limited dispersal abilities and thus may be affected by vicariant events. Fortunately, in comparison to many other Chinese animals, spiders have been well collected and studied. They are therefore ideal subjects for biogeographical studies (Fattorini, 2002).

Chinese spiders occur in 58 families (Table 1) and include 2858 species (see Appendix S1 in Supplementary Material). Herein, we define biogeographical regions of China based on the distributional patterns of spiders by applying a parsimony analysis of endemicity (PAE; Rosen, 1988; Rosen & Smith, 1988).

MATERIALS AND METHODS

Areas

A map of China was initially divided into 294 quadrats of 2° latitude by 2° longitude without consideration of physiographical features (Fig. 1). Many neighbouring quadrats had very similar climatic and geological characteristics, whereas other quadrats contained considerable physiographical and climatic variation. In addition, collecting efforts were inadequate in some quadrats. It was therefore desirable subjectively

Table 1 Numbers of the currently valid spider genera and species occurring in China.

Family	No. of genera	No. of species
Agelenidae C. L. Koch, 1837	4	22
Amaurobiidae Thorell, 1870	19	206
Anapidae Simon, 1895	3	3
Anyphaenidae Bertkau, 1878	1	2
Araneidae Simon, 1895	41	335
Atypidae Thorell, 1870	2	8
Clubionidae Wagner, 1887	1	80
Corinnidae Karsch, 1880	8	36
Ctenidae Keyserling, 1877	3	5
Ctenizidae Thorell, 1887	3	11
Cybaeidae Banks, 1892	2	7
Deinopidae C. L. Koch, 1850	1	1
Dictynidae O. P.-Cambridge, 1871	11	36
Dipluridae Simon, 1889	1	1
Dysderidae C. L. Koch, 1837	1	1
Eresidae C. L. Koch, 1851	1	2
Filistatidae Ausserer, 1867	3	17
Gnaphosidae Pocock, 1898	30	153
Hahniidae Bertkau, 1878	2	17
Hersiliidae Thorell, 1870	1	8
Hexathelidae Simon, 1892	1	8
Hypochilidae Marx, 1888	1	1
Leptonetidae Simon, 1890	1	15
Linyphiidae Blackwall, 1859	112	274
Liocranidae Simon, 1897	4	6
Liphistiidae Thorell, 1869	1	12
Lycosidae Sundevall, 1833	21	259
Mimetidae Simon, 1881	2	14
Miturgidae Simon, 1885	2	30
Nemesiidae Simon, 1892	3	6
Nesticidae Simon, 1894	1	5
Oecobiidae Blackwall, 1862	2	8
Oonopidae Simon, 1890	8	19
Oxyopidae Thorell, 1870	3	31
Palpimanidae Thorell, 1870	1	1
Philodromidae Thorell, 1870	3	47
Pholcidae C. L. Koch, 1851	7	40
Pisauridae Simon, 1890	6	28
Prodidomidae Simon, 1884	1	1
Psechridae Simon, 1890	2	11
Salticidae Blackwall, 1841	88	436
Scytodidae Blackwall, 1864	2	11
Segestriidae Simon, 1893	2	5
Selenopidae Simon, 1897	1	4
Sicariidae Keyserling, 1880	1	3
Sparassidae Bertkau, 1872	8	51
Telemidae Fage, 1913	1	3
Tetragnathidae Menge, 1866	17	77
Theraphosidae Thorell, 1870	4	5
Theridiidae Sundevall, 1833	36	270
Theridiosomatidae Simon, 1881	1	3
Thomisidae Sundevall, 1833	30	167
Titanoecidae Lehtinen, 1967	3	11
Trochanteriidae Karsch, 1879	1	4
Uloboridae Thorell, 1869	6	23

Table 1 Continued

Family	No. of genera	No. of species
Zodariidae Thorell, 1881	4	15
Zoridae F. O. P.-Cambridge, 1893	1	3
Zoropsidae Bertkau, 1882	2	3

to combine or divide some quadrats into biologically similar areas. Because it was very likely that these physiographical features would influence the distributions of species (Crisci *et al.*, 2003), adjacent quadrats that had very similar topographical characteristics were combined (cf. Fan, 1990). In doing so, natural barriers to dispersal were used to identify and separate dissimilar physiographic areas within and between quadrats. Sometimes these barriers corresponded to pre-existing subdivisions, such as provinces, districts and ecoregions. For example, combined quadrats with similar topographic characteristics formed the following areas: Inner Mongolia Plateau (area A10), Sichuan basin (A15), Qinghai-Tibetan Plateau (A11 and A21), Yunnan-Guizhou Plateau (A27, and A16), islands (A26 and A23), river deltas (A24 and A04), and mountains (A22). Other areas were designated on the basis of natural barriers, including the following: A21 was separated from A19 along the Karakorm Mountains; A21 was divided from A11 along the Tanggula Mountains; A15 was separated from A11 along the Hengduan Mountains; and A27 was isolated from adjacent regions along the Yunnan-Guizhou Plateau. The remaining areas were either combined because the distributional data of spiders indicated similarity with their surrounding areas, such as in separating area A28 from A05, A09 and A14, or divided on the basis of topographic characteristics, e.g. A19.

The combining and splitting of the 294 quadrats reduced the total number of study areas to 28. As an empirical test of validity, the new areas were compared with the distributions of species of spiders. This test revealed a good correspondence between the study areas and the distributions of many species. Consequently, this approach probably obtained the optimal results (Morrone & Escalante, 2002).

In total, 28 biological and physiographical areas (Fig. 1) were evaluated by PAE. The inclusion of geographically larger and smaller quadrats did not affect the analyses because PAE does not require all quadrats to be equal in size and shape (Posadas, 1996).

Distribution matrix

Detailed distributional data were obtained from both the literature and the collections at the Chinese Academy of Sciences, Beijing. The initial data set included 2858 species of Chinese spiders. A taxon/area data matrix scored the presence of a species in an area as '1' and the absence as '0'. Ambiguous distributional data were clarified from unpublished dissertations, or the ambiguity was coded as '?'. In total, 1809 species were removed from the analysis because their distributional data were not useful; these species either occurred in a single area only, and thus appeared as phylogenetically uninformative autapomorphies, or they occurred in all areas (Wiley, 1981). An additional 91 species were removed owing to inadequate distributional information. Areas were required to be grouped and defined by at least two species of spiders. These areas were delimited and mapped (Morrone, 1994). Thus, data from 958 species were included in the analysis (Appendix S2).

The data set contains 958 species and 5012 detailed collection records. At least 300 records occur in areas A02,

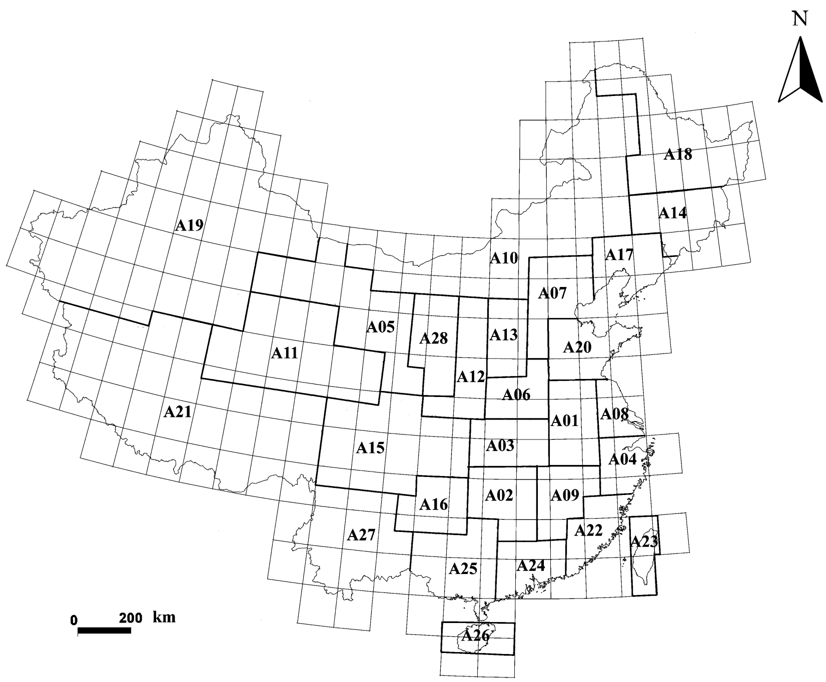

Figure 1 Map of China (excluding islands in the South China Sea) showing the 28 areas (A01–A28) used in the analysis after pooling 294 quadrats of 2° longitude by 2° latitude, primarily based on topographical characteristics.

Table 2 The number of species of spiders occurring in each of the areas defined for China.

Area	Number of species
A01	152
A02	343
A03	205
A04	306
A05	199
A06	143
A07	261
A08	92
A09	131
A10	169
A11	176
A12	191
A13	176
A14	221
A15	302
A16	122
A17	142
A18	96
A19	211
A20	167
A21	171
A22	185
A23	196
A24	158
A25	151
A26	104
A27	176
A28	66

A04, and A15. Areas A03, A07, A14, and A19 contain from 200 to 300 records. Most areas, namely A01, A05, A06, A09, A10, A11, A12, A13, A16, A17, A20, A21, A22, A23, A24, A25, A26, and A27, have from 100 to 200 records of spiders. In the last two areas, A08 and A28, there are fewer than 100 records (Table 2).

Parsimony analysis of endemicity

PAE encapsulates the natural patterns of biotic distributions (Rosen, 1988; Rosen & Smith, 1988). It is analogous to a cladistic analysis, with areas equivalent to taxa and the occurrences of species forming the characters. Groups are formed by the occurrence of shared species. A hypothetical area that had no taxa was used as an outgroup to root the cladogram (Rosen, 1988; Rosen & Smith, 1988; Cracraft, 1991; Morrone & Crisci, 1995; Geraads, 1998; Waggoner, 1999; Morrone & Escalante, 2002; Brooks & van Veller, 2003; Porzecanski & Cracraft, 2005). Although PAE can provide a summary of localities, areas of endemism, or quadrats (Crisci *et al.*, 2003), herein it is applied to combined quadrats only.

The taxon × area data matrix was analysed with the criterion of maximum parsimony using PAUP* 4.0 (Swofford, 1998) with a heuristic search of 1000 replicates and random sequence addition. Bootstrapping (Felsenstein, 1985) with 100 replications and 1000 random sequence additions was used to estimate the confidence intervals for the recovered nodes. All characters were weighted equally.

RESULTS

The parsimony analysis obtained four most-parsimonious trees (3143 steps; CI = 0.3048; RI = 0.4079). The trees differed in the positions of areas A05 and A23. Area A05 was included either within clade A10 + A19 + A11 + A21 or at its base. The second arrangement was more strongly supported, with a bootstrap support value of 40% as opposed to 12% for the first. Area A23 clustered either as ((A23, A27) A16) or as (A23 (A15 (A02, A04))). In the first arrangement the bootstrap support value was 13%, and in the second possibility the bootstrap support value was 11%. The arrangement with the highest bootstrap proportion for areas A05 and A23 was selected for discussion (Fig. 2).

Two clear groups, B and C (Fig. 2), were discovered by the analysis. The bootstrap proportion of group B (90%) was nearly twice that of group C (44%). When mapped, clades B and C corresponded to a geographical barrier within the confines of the Qinling Mountains and Huai River, and east of the Hengduan Mountains (Fig. 3). In group B, four clades were identified: B_1 (A28), B_2 (A05 + A10 + A11 + A19 + A21), B_3 (A06 + A07 + A12 + A13 + A20), and B_4 (A14 + A17 + A18) (Fig. 2). Clade B_2 had a bootstrap proportion of 40%. It contained three sub-clades, A05, A10 + A19, and A11 + A21, each of which corresponded to a landform. For example, A10 + A19 were contained within the steppe and desert of north-western China, and A11 + A21 corresponded to the Tibetan plateau. Area A05 included the transition zone between A10 + A19 and A11 + A21. Having the greatest bootstrap support of any clade (75%), B_3 corresponded to Central Northern region. Clade B_4 corresponded to Eastern Northern region, including the Changbai and Xiao Xingan mountains (Fig. 3); its bootstrap support value was 49%.

Five clades were identified in group C: C_1 (A09), C_2 (A01 + A02 + A03 + A04 + A15 + A08), C_3 (A22 + A24), C_4 (A16 + A23 + A27), and C_5 (A25 + A26) (Fig. 2). Bootstrap proportions of C_1 to C_4 were smaller than the values obtained for B_2, i.e. <40%. Clade C_5 had the greatest bootstrap value (75%). The range of C_2, Central region, included areas north of the Qinling and Hengduan mountains and the Huai River, and regions south of the Yangtze River. C_3, Eastern Southern region included the south-eastern coast. Areas A27 and A16 and area A23 (Taiwan Island) formed two sub-clades in C_4. Clade C_5 contained areas with similar arachnifaunas: areas A25 and A26 (Hainan Island).

Based on the patterns of distributions of the spiders, seven major regions can be recognized in China: Western Northern region (B_2), including the Tibetan Plateau subregion and Inner Mongolia-Xinjiang subregions; Central Northern region (B_3); Eastern Northern region (B_4); Central region (C_2); Eastern Southern region (C_3); Western Southern region (C_4); and

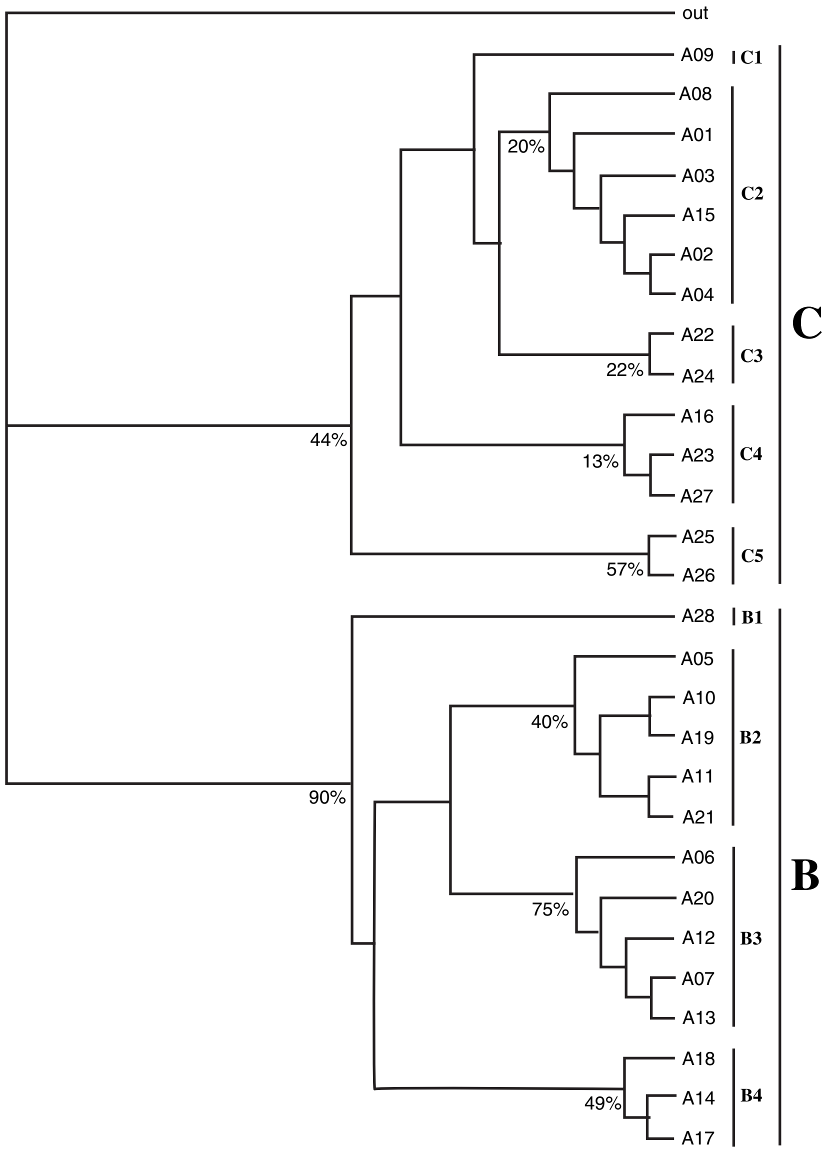

Figure 2 Selected area cladogram illustrating the relationships of the 28 areas based on a parsimony analysis of 958 distributions shared by species of spiders. Numbers below the lines indicate bootstrap proportions. Outgroup: 'out'.

Central Southern region (C_5). Clades B_1 and C_1 exhibited no clear patterns, and their associations remained ambiguous.

Western Northern region – Clade B_2

The Western Northern region includes the Tibetan Plateau subregion (A11 + A21) and north-western provinces (Xinjiang and Inner Mongolia; A10 + A19). Although these subregions share a similar, arid climate, they have two dramatically different topologies. To the south, the Tibetan Plateau subregion has an average elevation of about 4000 m and a typical continental climate. It receives more sunshine than any other region of the country, but is quite cold as a result of its high elevation. Glaciers and permanent snowfields abound, and the central and north-western parts of the plateau have permafrost soils. There are numerous lakes and marshes, with many lakes being saline. More than 320 species of spiders have been recorded in this subregion. These species belong to 33 families (Appendix S3), of which the Lycosidae (67 species), Salticidae (44 species) and Theridiosomatidae (27 species) dominate.

The northern part of this region, the Inner Mongolia-Xinjiang subregion, consists of the Xinjiang and Inner Mongolia provinces. Steppe and deserts dominate. It includes some of the hottest and driest areas on Earth. The climate ranges from being cool-temperate in the north to temperate and warm-temperate in the south, and ranges dramatically from being arid in the west to sub-humid in the east. About 340 species of spider have been recorded in this subregion. They belong to 34 families (Appendix S3), of which the Lycosidae (75 species), Salticidae (55 species), Araneidae (29 species) Theridiosomatidae (23 species) and Philodromidae (20 species) dominate.

Central Northern region – Clade B_3

This region includes the low-lying basin of the Yellow River. It has a warm, temperate, relatively dry climate. Much of the land has been developed for agricultural use, and only a few patches of forest remain. About 300 species of spiders have been recorded in this region, but no species appears to be endemic. Species in this region belong to 35 families (Appendix S3), of which the Lycosidae (64 species) and Salticidae (48 species) are most speciose.

Eastern Northern region – Clade B_4

The Eastern Northern region consists of the Xiao Xingan and Changbai mountains. The climate is humid and cold-temperate. Several forest species of birds and mammals are similar to those found in northern Europe, Asia and North America (Zhao & Adler, 1993). About 290 species of spiders have been recorded in this region, but none of them is endemic. Species belong to 33 families (Appendix S3), of which the Araneidae (25 species) dominates.

Central region – Clade C_2

The Central region consists of the Yangtze River and its tributaries. It has a subtropical monsoonal climate with plentiful rainfall. The four landscapes in this region are mountains, hills, basins, and plains. The mountains, which are located in the west, slope eastwards, forming the alluvial deposits of the Yangtze River. Spiders in this region belong to 34 families (Appendix S3), of which the Lycosidae (58 species) and Araneidae (26 species) are most abundant.

Eastern Southern region – Clade C_3

The Eastern Southern region consists of Guangdong and Fujian provinces. Generally, its staircase topography descends from the north-west to the south-east seaboard. Its principal mountains run from the north-east to the south-west. Long, narrow plains occur along the coast. Marked climatic differences occur between the north and south, coastal and inland regions, and valleys and mountains. Coastal regions frequently receive typhoons between May and November. About 310 species have been recorded but none is endemic. They are assigned to 33 families (Appendix S3), of which the Lycosidae (63 species), Salticidae (57 species) and Araneidae (31 species) are most speciose.

Western Southern region – Clade C_4

The Western Southern region includes two distinct landforms at the same latitude: Taiwan Island and the Yunnan-Guizhou Plateau. The plateau is contiguous with the Qinghai-Tibetan Plateau to the north-west. High, north-western regions descend south-eastwardly. A great difference in elevation occurs between these regions. In the eastern Yunnan Plateau, karst topography occupies wide areas and involves spectacular pinnacles, caverns and subterranean streams. The western Yunnan valley, part of the Hengduan Range, consists of many intermontane valleys arranged vertically from north to south and from west to east. From north to south, the complicated terrain results in three climatic zones: temperate, subtropical and tropical. These climatic zones are distributed from low to high elevations over four regions: low, hot river valley ba zi (small upland plains), mountain areas, and cold highlands. These form a peculiar ‘three-dimensional’ climate.

Taiwan Island is close to the South-eastern Central area (C_3). About 270 species of spiders are found in this region, none of them endemic. They belong to 31 families (Appendix S3), of which the Salticidae (40 species) and Araneidae (32 species) dominate.

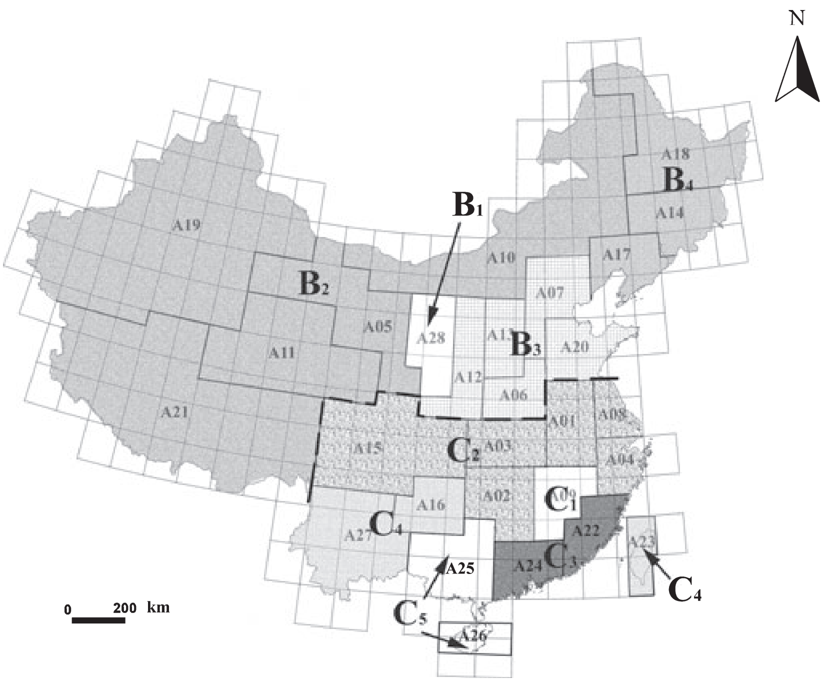

Figure 3 Generalized pattern of the distribution of Chinese spiders based on a parsimony analysis of endemicity. The broken line is the boundary between clades B and C. Different backgrounds indicate the clades in Fig. 2. B_1, area A28; B_2, Western Northern region; B_3, Central Northern region; B_4, Eastern Northern region; C_1, area A09; C_2, Central region; C_3, Eastern Southern region; C_4, Western Southern region; C_5, Central Southern region.

Central Southern region – Clade C_5

The Central Southern region includes Hainan Island and the Guangxi Basin. Hainan Island consists of hills, mountains, and arid tablelands. The north-western portion of the Guangxi Basin is part of the Yunnan-Guizhou Plateau. Its northern portion is locked within the Jiuwandashan, Damiao and Tianping mountains. North-eastern Guangxi Basin is part of the Nanling Mountains, comprising the Yuechengling, Haiyang, Dupangling and Mengzhuling ranges that extend south-westwards parallel to one another. The Yunkaidashan, Liuwandashan, Shiwandashan and Daqingshan mountains are situated in the south. The majority of the mountains are 1000–1500 m above sea level. The Central Southern region has a subtropical monsoonal climate with long summers, warm winters, plentiful rainfall, and frequent rainstorms and typhoons in the summer and autumn. About 290 species of spiders occur in this region. They belong to 32 families (Appendix S3), of which the Lycosidae (62 species), Salticidae (43 species), and Araneidae (30 species) are the most speciose.

DISCUSSION

Spider distributional patterns and the geological provinces of China

The archipelago model of orogenesis (Hsü & Chen, 1999) divides China into six geological provinces: Laurentian/Cathaysian Southern and South-western Margin, North-western China, Central China, Southern China, Tibet, and Pacific China. This arrangement incorporates 31 map-units based on 200 tectonic-facies (Hsü & Chen, 1999). These geological provinces broadly match the distributional patterns of spiders. For example, the North-western China geological province, excluding the Northern China region, is comparable with the Central Northern region (clade B_3) with the Inner Mongolia-Xinjiang subregion. The northern part of the Pacific China geological province is similar to the Eastern Northern region (clade B_4). The Laurentian/Cathaysian Southern and South-western Margin geological province combined with the Tibetan geological province corresponds to the Tibetan Plateau biogeographical subregion. The Central China geological province is similar to the Central region (clade C_2). The Southern China geological province generally corresponds to the Eastern Southern (clade C_3), Western Southern Central (clade C_4), and Central Southern (clade C_5) regions combined.

A comparison of the geological provinces and the distributional patterns of spiders reveals that the spiders occur south of the geological provinces. This anomaly may be explained by two hypotheses: distributional stability, and post-orogenic change. In the distributional stability hypothesis, the patterns of spider distribution did not change after the last plate movement. This scenario seems extremely unlikely because orogenesis may be the only way to universally influence biogeographical patterns. The most recent orogenesis occurred over 0.78 Ma (Wan, 2003). Although this amount of time is sufficient to influence the distributional patterns of spiders, the spiders occur south of the geological provinces. In contrast, the post-orogenic-change hypothesis stipulates that the patterns of spider distribution were altered after the last plate movement. In this case, dispersal, extinction, invasion, and/or speciation are important factors. Pleistocene glaciation must have caused dispersal, extinction, invasion, or speciation of organisms. Of these two hypotheses, the post-orogenic-change hypothesis provides the only reasonable explanation of the distribution of spiders relative to the geological provinces.

Spider distributional patterns and other biogeographical patterns

Different organisms may share a general distribution pattern because they are influenced by the same geological history. In order to infer a general pattern, it is necessary to compare patterns based on different groups of organisms, such as the traditional biogeographic patterns obtained by Zhang (2004) and Xie *et al.* (2004), with the patterns of spiders. Interestingly, five areas are congruent: the Tibetan Plateau, Central Northern, Eastern Northern, Western Northern (excluding Tibetan Plateau), and Southern regions.

Some differences occurred between our results and those of Zhang (2004) and Xie *et al.* (2004). First, Xie *et al.* and Zhang separated the Hengduan Mountains and the south-facing Himalayas from the Tibetan Plateau subregion, unlike our regions. The separation was based on the distributions of various mammals and plants, as well as on particular geographical characteristics. This discrepancy may be a result of the general absence of fine-scaled distributional data for spiders.

Second, distributional patterns of spiders revealed novel borders between the Eastern Northern region (Clade B_4) and the Inner Mongolia-Xinjiang subregion. The biological associations of the Da Xingan Mountains are controversial. Plants in the Xiao Xingan and Changbai mountains are similar, but differ from plants in the Da Xingan Mountains (Xie *et al.*, 2004). Superimposing the analysis of Xie *et al.* (2004) on our data, the Da Xingan Mountains are placed with the Inner Mongolia-Xinjiang subregion of spiders. In contrast, Zhang (2004) suggested that the Da Xingan Mountains should be placed in our Eastern Northern region (Clade B_4), based on mammalian distributions. This difference may be attributable to the taxa analysed. Plants and spiders have relatively poor migratory abilities and may be more affected by vicariant events (Fattorini, 2002).

Third, southern China, including clades C_2, C_3, C_4, and C_5 (Fig. 3), has a complex pattern. This area was divided into the Central and Southern regions with six subregions by Zhang (2004). Xie *et al.* (2004) considered this area to be one region with three subregions. The position of the islands complicates division into subregions. Zhang (2004) suggested that each island was a subregion, but Xie *et al.* (2004) asserted that they constituted a single subregion. Our analyses suggest that the islands have had geologically recent biological contact with the mainland. Therefore, we suggest that the biogeographical patterns in southern China are reticulate. The reticulation is best explained by sea-level changes caused by Pleistocene glaciation (Yang, 2004): coastlines advanced and retreated with each glacial cycle. Reticulate area relationships cannot be analysed by PAE (Brooks & van Veller, 2003), although PAE-PCE, i.e. PAE with progressive character elimination (García-Barros *et al.*, 2002), may help to unravel reticulate relationships. Notwithstanding, it seems preferable to consider southern China as a single area without subregions.

ACKNOWLEDGEMENTS

This paper benefited greatly from comments from Daniel R. Brooks (University of Toronto, Canada), Jinzhong Fu (University of Guelph, Canada), Xinping Wang (University of Florida, Gainesville, USA), and Jun Chen (Chinese Academy of Sciences, Beijing, China). This study was supported by the National Natural Sciences Foundation of China (NSFC-30270183, 30370263, 30310464, 30470213, 30499341), by the National Science Fund for Fostering Talents in Basic Research (NSFC-J0030092), by the Beijing Natural Science Foundation (6052017), partly by the Kadoorie Farm and Botanic Garden, Hong Kong Special Administrative Region, China, and partly by the Natural Sciences and Engineering Research Council of Canada (discovery grant A3148).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Appendix S1 List and distribution of Chinese spiders.
Appendix S2 The data matrix for PAE analysis.
Appendix S3 Numbers of species of spiders per region.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01843.x

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Editor: Malte Ebach