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Coevolution of brachiopod Boreal Realm and Pangea

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ABSTRACT

The Boreal Realm originated in the early Carboniferous; the realm became more firmly established during the late Carboniferous and early Permian, and peaked in the middle Permian before decaying in the late Permian. In the early Carboniferous, the geographic distribution of the Boreal Realm was latitudinally narrow, and many brachiopod genera of the realm were also common in the Tethys Realm. The Boreal Realm faunas were, however, also characterized by many geographically and temporally restricted genera. The Boreal Realm was well developed in the late Carboniferous, as represented by the continued expansion of the geographical ranges and numbers of occurrences of many Permian characteristic Boreal Realm genera. In the early Permian, the geographic distribution of the Boreal Realm expanded further, as did the distribution of characteristic Boreal Realm genera. In the middle Permian, the geographic distributions of the Boreal Realm had expanded to their greatest extent, and the characteristic Boreal Realm genera were most abundant and diverse. In the late Permian, the cool-water characteristic genera, which flourished during the Carboniferous to middle Permian, disappeared in these areas, and resulted in the decay of Boreal Realm.

The development of the Boreal Realm was closely related to events leading to the formation of Pangea, in which a variety of plates (Laurussian, Siberian, etc.) were continuously drifting northwards; some plates/blocks entered middle- and high-latitudinal regions and were located in cool climatic environments. During the evolution of Pangea, the Siberian, Kazakhstan, and Eastern European plates were continuously located in the center of the Boreal Realm; the Barents Ocean developed to the west and the Paleo-Asian Ocean developed to the east of these plates. This configuration of oceans and continents differentiated the eastern Central Asia Region and the western Barents Region. In the Paleo-Asian Ocean tectonic domain, the northern branch of the Paleo-Asian Ocean was surrounded by the Siberian plate, the Kazakhstan plate, and the Jiamusi–Mongolia Block, and named the Mongolia–Okhotsk Ocean. The Mongolia–Okhotsk brachiopod fauna developed on the southern margin of the Mongolia–Okhotsk Ocean (i.e., the northeastern margins of the Siberian and Kazakhstan plates, and the northern margin of the Jiamusi–Mongolia Block), thus forming the Mongolia–Okhotsk Province. During the middle Permian, the Xar Moron Ocean was enclosed by the Jiamusi–Mongolia Block and the Kazakhstan, Tarim, and South China plates. On the southern margin of the Xar Moron Ocean (i.e., the southern margin of the Jiamusi–Mongolia Block), the Zhesi brachiopod fauna developed, and the Inner Mongolia Province was formed. During the Carboniferous–Permian, the Kolyma-Chukchi block, Siberian plate, and North American plate comprised the Barents Ocean tectonic domain. The Verkhoyansk brachiopod fauna developed on the northern margin of the Barents Ocean (i.e., on Verkhoyansk and the southwestern margin of the Siberian plate), thus forming the Verkhoyansk–Taymyr Province. Starting in the late Carboniferous, a cool-water brachiopod fauna developed on the southern margin of the Barents Ocean (i.e., the northern margin of the North American plate and the northern margin of the Eastern European plate), thus forming the Yukon–Pechora Province, the geographical range of which extended continuously with time.

1. Introductions

During the Carboniferous–Permian, a cool-water brachiopod fauna appeared in middle- and high-latitudinal regions, thus marking the appearance of a unique biogeographic realm, the Boreal Biogeographic Realm (hereafter, Boreal Realm). Boreal Realm brachiopod faunas were first recognized by Stehli and Grant (1971), based on their study of Permian brachiopod faunas in the Axel Heiberg Islands; they proposed the concept of a cool-water Boreal Realm, a concept which was further developed by Stehli (1973). Subsequently, the Boreal Realm concept has been widely applied in studies of Late Paleozoic biogeography, especially with respect to Permian (Xu and Yang, 1988; Wang, 1994a; Grunt, 1995; Shi et al., 1995; Grunt and Shi, 1997; Shang and Jin, 1997; Shi, 1998; Tazawa, 1998; Shi and Grunt, 2000; Shi and Shen, 2000; Tazawa, 2001; Shi

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et al., 2002; Wang and Zhang, 2003; Shen et al., 2005; Tazawa and Chen, 2006; Wang and Zhang, 2008; Wang et al., 2008; Shen et al., 2009; Wang et al., 2012; Shen et al., 2013) and Carboniferous (Yang, 1988; Yang, 1990; Wang, 1994a, 1994b, 1996; Wang and Yang, 1998a; Li and Shen, in press) brachiopod faunas. On the other hand, this concept has been rarely applied to the paleobiogeography of Devonian brachiopods (Zhao, 1988).

Details surrounding the appearance of the Boreal Realm have not been thoroughly explored, and the mechanisms of formation of the realm have been scarcely addressed; developmental and evolutionary trends subsequent to the formation of the Boreal Realm have also received little attention. Thus, this paper presents a preliminary discussion regarding these issues.

2. Coevolution of the Boreal Realm and Pangea during the Early Carboniferous

2.1. The Boreal Realm during the Early Carboniferous

The Boreal Realm was in its infancy in the early Carboniferous. The geographic distribution of the realm was latitudinally narrow, and many brachiopod genera of the Boreal Realm were also common in the Tethys Biogeographic Realm (hereafter, Tethys Realm). The Boreal Realm faunas were, however, also characterized by many geographically and temporally restricted genera.

The early Carboniferous Boreal Realm comprised mainly the areas of Verkhoyansk, the Kuznetsk Basin, Rudny Altay, northern Junggar, and Chita (Fig. 1). According to our preliminary survey of the literature, the Boreal Realm was characterized by 41 brachiopod genera, and a number of genera have been recognized in two or more locations (*Hunanoproductus*, *Lanipustula*, *Nekhoroshevia*, *Orulgania*, *Septosyringothyris*, *Sphenospira*, and *Tomiopsis*). Among these 41 genera, some were also present in the late Carboniferous, such as *Lanipustula*, *Orulgania*, *Paeckelmanella*, *Praehorridonia*, *Taimyrella*, *Tomiopsis*, *Verkhojania*, and *Zaissania*. In this paper, these brachiopod genera are regarded as early Carboniferous characteristic genera (Fig. 1C).

Among the 41 characteristic genera of the Boreal Realm, some were present only in Verkhoyansk, such as *Andreaspira*, *Arktikina*, *Bailliena*, *Buxtoniella*, *Crassispirifer*, *Dictyoclostidae*, *Moderatoproductus*, *Nordathyris*, *Ovlatchania*, *Paeckelmanella*, *Praehorridonia*, *Sajakella*, *Taimyrella*, *Trifidorostellum*, *Tulathyris*, *Verkhojania*, and *Ziganella*, whereas others were present only in the Kuznetsk Basin–northern Junggar–Chita, such as *Absenticosta*, *Cmarotoechia*, *Hunanospirifer*, *Iniathyris*, *Levipustula*, *Mucrospirifer*, *Plactospira*, *Pseudorthotetes*, *Reticulatochonetes*, *Retzia*, *Seutepustula*, *Sphenospira*, *Steinhagella*, *Tenticospirifer*, *Tomilia*, *Tomiodendron*, *Ulbospirifer*, *Whidbornella*, and *Zaissania*. Thus, the Boreal Realm of the early Carboniferous can be divided into the Verkhoyansk Biogeographic Province (hereafter, Verkhoyansk Province) of the Barents Biogeographic Region (hereafter, Barents Region) and the Mongolia–Okhotsk Biogeographic Province (hereafter, Mongolia–Okhotsk Province) of the Central Asia Biogeographic Region (hereafter, Central Asia Region) (Fig. 1C).

The relationship between the faunas of the Boreal and Tethys realms was stronger than that between the Boreal and Gondwana realms. During the early Carboniferous, 57 genera appeared in both the Boreal Realm and the Tethys Realm; among them *Avonia*, *Echinoconchus*, *Dictyoclostus*, *Marginatia*, *Neospirifer*, *Ovatia*, *Plicochonetes*, *Pustula*, and *Torynifer* were common.

The early Carboniferous brachiopod fauna in the Kazakhstan–southern margin of the Jiamusi–Mongolia Block and in Europe, central and southern North America, and South China comprised 130 characteristic

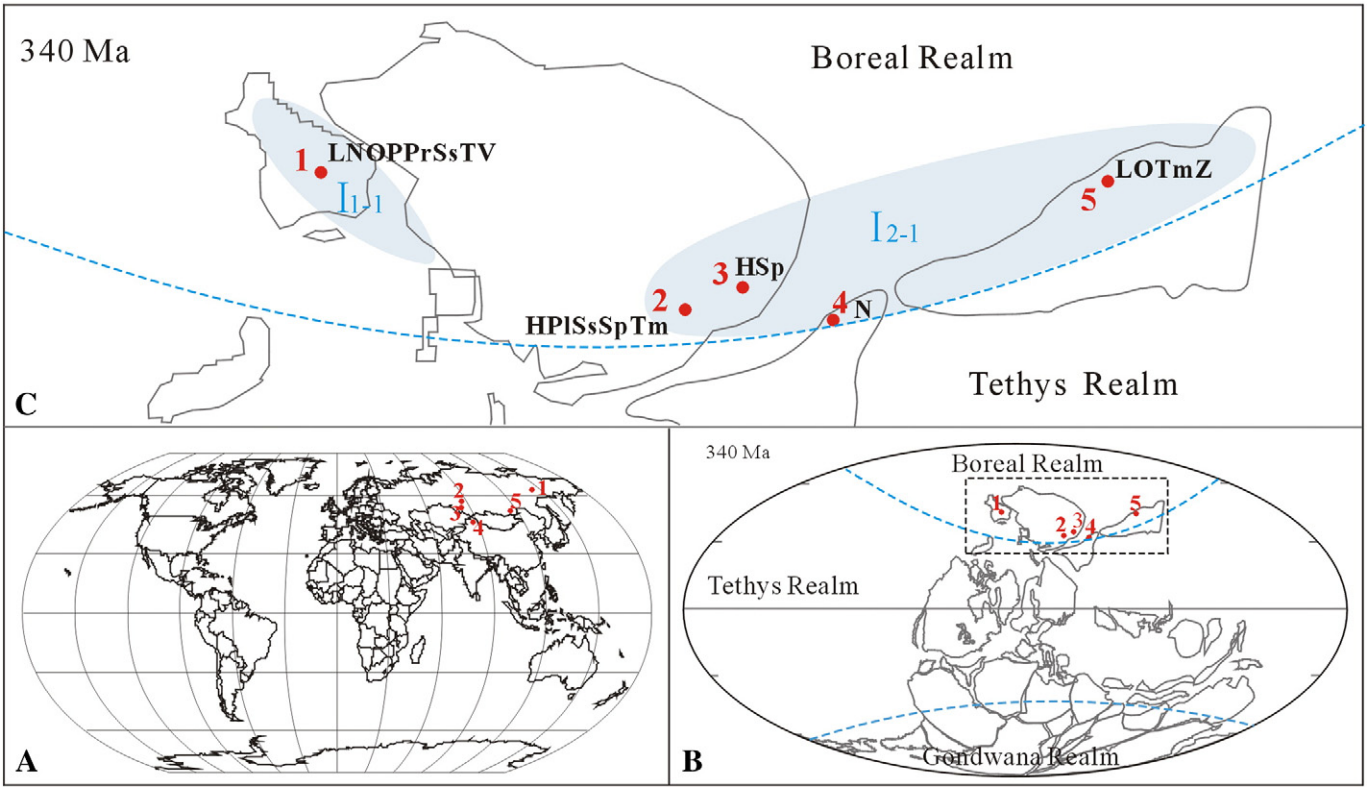

Fig. 1. Distribution of collection localities, characteristic brachiopod genera, and provinces of the early Carboniferous Boreal Realm. (A) Fossil locations on a present-day geographic map. (B) Fossil locations on a tectonopaleogeographic map (modified from Boucot et al., 2009). (C) Distributions of characteristic genera. Locations and sources of material (labeled in red): 1, Verkhoyansk (Abramov and Grigoryeva, 1983, 1986); 2, Kuznetsk Basin (Sarytcheva et al., 1963); 3, Rudny Altay (Gretchishnikova, 1966); 4, northern Junggar (Zhang et al., 1983); 5, Chita (Kotlyar, 2002). Codes for characteristic genera: H, *Hunanospirifer*; L, *Lanipustula*; N, *Nekhoroshevia*; O, *Orulgania*; P, *Paeckelmanella*; Pl, *Plactospira*; Pr, *Praehorridonia*; Ss, *Septosyringothyris*; Sp, *Sphenospira*; T, *Taimyrella*; Tm, *Tomiopsis*; V, *Verkhojania*; Z, *Zaissania*. Codes for biogeographical units (labels and areas shaded blue): I_{1-1}, Verkhoyansk Province of the Barents Region; I_{2-1}, Mongolia–Okhotsk Province of Central Asia Region.