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Paleobiogeography of the pectinid bivalve *Neithea*, and its pattern of step-wise demise in the Albian Northwest Pacific

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ABSTRACT

The pectinid bivalve genus Neithea is one of the most important indicators for understanding the biogeographic relationships between the Tethyan Realm and North Pacific Province during the Cretaceous Period. Changes in temporal species diversity, endemic/widespread species composition, and origination and demise ratios of Neithea at each Cretaceous stage boundary in the Northwest Pacific were analyzed from a biogeographic perspective. Neithea is continuously present in the Northwest Pacific during the Berriasian to late Albian time interval. Species diversity reached its maximum in the late Aptian, being correlated with the global warming phase. Step-wise demise of Neithea in the Northwest Pacific during the Albian is subdivided into three stages: the late Aptian/early Albian, early Albian/middle-late Albian, and late Albian/ early Cenomanian. Thereafter, Neithea disappeared in the Northwest Pacific and never reappeared. This pattern is the reverse of the Albian diversification of Neithea in the Mediterranean, and also contrary to the Mid-Cretaceous global warming trend. Demise of Neithea in the Northwest Pacific occurred simultaneously with the step-wise demise of Mesogean taxa (e.g., rudists) which strongly supports the idea that the Northwest Pacific gradually became independent from the Tethyan Realm during the Albian. It also suggests a long-term deterioration of the faunal interchange between the North Pacific Province and Tethyan Realm throughout the Late Cretaceous. This biogeographic change was possibly caused by Albian "cooling" and changes in oceanic flow/heat transport in the Northwest Pacific.

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1. Introduction

Mid-Cretaceous is a well-documented greenhouse period of global importance during the Earth's history (Johnson et al., 1996; Clarke and Jenkyns, 1999; Wilson and Norris, 2001; Huber et al., 2002; Steuber et al., 2005). The typical Tethyan biota (Mesogean taxa in the sense of Masse, 1992) (e.g., rudists and orbitolinid foraminifers), extensively flourished within tropical shallow marine settings in the world's oceans throughout the Cretaceous, and therefore are regarded as essential indicators of tropical realm and climate (Masse, 1992). Recently, Iba and Sano (2007) summarized the Cretaceous record of Mesogean taxa (sensu Masse, 1992) mainly from clastic sequences of the Northwest Pacific, and described their demise during latest Aptian–middle Albian. Iba and Sano (2007) explained this bio-event by means of vicariance, which led to the establishment of the North Pacific Province (Jeletzky, 1971) being independent from the Tethyan

Realm. The North Pacific Province was clearly distinguishable during the Late Cretaceous Epoch. Late Cretaceous bivalve faunas in the Northwest Pacific contain many endemic taxa, which first appeared in the Albian (e.g., Hayami and Yoshida, 1991; Tashiro, 2000). Thus it is expected that remarkable biotic changes occurred in the mid-Cretaceous Pacific, already at that time the world's largest aquatic reservoir.

In addition to Mesogean taxa, some bivalves (e.g., *Neithea* and *Chondrodonta*), for which a term "Tethyan non-rudist bivalves" was coined (Dhondt, 1992; Dhondt and Dieni, 1992), inhabited warm shallow marine environments, together with Mesogean taxa. For this reason, they are also considered as a good indicator of the Cretaceous Tethyan Realm and warm climatic environment. The pectinid bivalve *Neithea*, has often been used for Cretaceous biogeographical studies in Europe, the Mediterranean, Western Interior Seaway, and South Atlantic (e.g., Dhondt, 1981, 1985, 1992; Dhondt and Dieni, 1991, 1992; Kauffman et al., 1993; Andrade et al., 2004). This genus commonly occurs in the Cretaceous shallow marine calcareous deposits in the Northwest Pacific, and has the most abundant and continuous record among the Tethyan non-rudist bivalves in this region (e.g., Hayami, 1975; Hayami and Noda, 1977; Iba and Sano, 2007). There are many

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taxonomic, stratigraphic, and paleontological studies of *Neithea* in the Northwest Pacific, and therefore, we can easily compare its spatiotemporal distribution pattern in the Northwest Pacific with other regions. Although a mid-Cretaceous "local extinction" of *Neithea* in the Northwest Pacific has been recognized (Hayami, 1989; Hayami and Yoshida, 1991) as an important biotic change in the Cretaceous Pacific, its detailed process, timing, and paleobiogeographic significance however remain unknown. The present study analyses statistically all the available data on *Neithea* in the Northwest Pacific, in order to elucidate its spatiotemporal occurrence pattern. Furthermore, we compare the spatiotemporal distribution patterns of *Neithea* in the Northwest Pacific with those in Mediterranean region, and other contemporaneous biotic changes in the Northwest Pacific. Finally, we discuss the mid-Cretaceous paleobiogeographic changes of marine biota in the Northwest Pacific and its possible causes.

2. Note on taxonomy of Neithea in the Northwest Pacific

Cretaceous shallow marine deposits are widely distributed in the Northwest Pacific margin (Taiwan–Japanese Islands) which occupied the eastern margin of the Asian Continent during this period. These yield numerous well-preserved macro- and microfossils from various horizons. Since the first report of *Neithea* from the Northwest Pacific by Yabe et al. (1926), *Neithea* has been reported from many localities in this region (Fig. 1 and Table 1). Although Cretaceous marine deposits are distributed in Northeast China and Far East Russia (Sikhote-Alin and Kamchatka), there is no documented occurrence of *Neithea* in these regions. Several species of *Neithea* were reported from the mid- to Upper Cretaceous in Tibet and Tarim Basin, western China (e.g., Wen, 1999). However, since these seas were not connected directly to the Northwest Pacific, but to the Tethys Sea (e.g., Chen, 1987; Wen, 1999), these occurrences are not discussed in this paper.

Detailed taxonomic studies of *Neithea* species from the Northwest Pacific have been done by Hayami (1965) and Hayami and Kawasawa (1967). Dhondt (1973) regarded several endemic species described

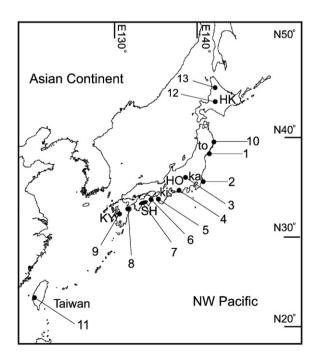


Fig. 1. Occurrences of *Neithea* in the Cretaceous of Northwest Pacific. All locality numbers are compatible with those from Table 1. HK; Hokkaido Island, HO; Honshu Island, SH; Shikoku Island, KY; Kyushu Island, to; Tohoku area, ka; Kanto area, ki; Kinki area.

by Hayami (1965) as junior synonyms of European species. Subsequently, Hayami (1975) and Hayami and Noda (1977), with reference to Dhondt's (1973) interpretation, revised the taxonomy of Japanese and Taiwanese species and described eight species from this region (*N. aketoensis*, *N. atava*, *N. ficalhoi*, *N. kochiensis*, *N. matsumotoi*, *N. nipponica*, *N. notabilis*, *N. syriaca amanoi*). Subsequently, Tashiro and Kozai (1986) described one new species (*N. hanourensis*). Species of *Neithea* from Northwest Pacific are characterized by two well-developed secondary ribs between each two tripartite principal ribs, and have been identified as the Mediterranean species *N. ficalhoi* (Choffat, 1888) (Hayami, 1965; Hayami and Noda, 1977; Tashiro and Kozai, 1986; Tanaka et al., 1999, 2002; Kawano et al., 2002), which recently has been synonimized with *N. alpina* (d'Orbigny, 1847) (Andrade et al., 2004). Herein we followed the interpretation of Andrade et al. (2004).

The taxonomic status of N. kochiensis and N. aketoensis described from the Aptian deposits of Japan by Hayami (1965) and Hayami and Kawasawa (1967) remains unclear due to scarce and poorly preserved material. N. kochiensis was proposed by Hayami and Kawasawa (1967) based on a poorly preserved inner mould of a specimen that possess no prominent secondary ribs. The feature of secondary ribs of N. kochiensis is possibly a misinterpretation due to its poor preservation. Well-preserved specimens of alleged N. kochiensis were reported by Tanaka et al. (1996), but the rib morphology and distribution pattern of these specimens resembles that of N. atava (Roemer, 1839), a species which displays worldwide distribution inclusive of the Japanese Islands. N. aketoensis Hayami (1965) was based on a single specimen from the upper Aptian of the Hiraiga Formation on the Pacific coast of the Northeast Honshu (Loc. 10 in Fig. 1). We re-examined the type specimen, and concluded that the rib morphology and its distribution pattern both on the inner mould and external shell surface resembled those of N. nipponica Hayami (1965). Therefore, N. aketoensis should be considered as a junior synonym of N. nipponica. Taking into account the discussion above we excluded N. kochiensis and N. aketoensis from further consideration in this paper. Detailed taxonomic revision of these two species will be provided elsewhere.

3. Material and methods

Eight species of *Neithea* (*N. alta*, *N. atava*, *N. hanourensis*, *N. notabilis*, *N. matsumotoi*, *N. alpina*, *N. syriaca amanoi*, *N. nipponica*) reported from more than 60 publications in Taiwan–Japanese Islands (see Appendix) are considered in the present study. We have not taken into account the species of *Neithea* left in open nomenclature. The objectives are to clarify temporal diversity changes, demise and origination ratios, and endemic/widespread species compositions in the surveyed region. The Aptian–Albian time interval is a crucial period for marine paleobiogeography in the Northwest Pacific (e.g., Iba and Sano, 2006, 2007) and so the interval is analyzed to the substage level. However, because of difficulty in recognizing the middle Albian stage in the all circum-North Pacific regions due to the paucity of index fossils, we treated middle and late Albian jointly.

We calculated demise and origination ratios at each stage and/or substage boundary, and then attributed the biogeographic-type of species (i.e., endemic or widespread species) for each stage and substage. Demise ratio (DR) and origination ratio (OR) are defined as follows: DR=(number of preexisting species absent above each boundary)/(total number of species below each boundary), (R=(number of successor species not present below each boundary)/(total number of species above each boundary). The ratios of endemic and widespread species were examined based on previous biostratigraphic, biogeographic and taxonomic studies of each species in the Europe, Mediterranean, Caribbean–Western Interior Seaway, and Atlantic (Dhondt, 1973, 1981, 1982, 1992; Dhondt and Dieni, 1991, 1992; Kauffman et al., 1993; Bogdanova and Yanin, 1995; Kues, 1997; Andrade et al., 2004). Endemic species are defined here as species that

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