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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.

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 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), OR=(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

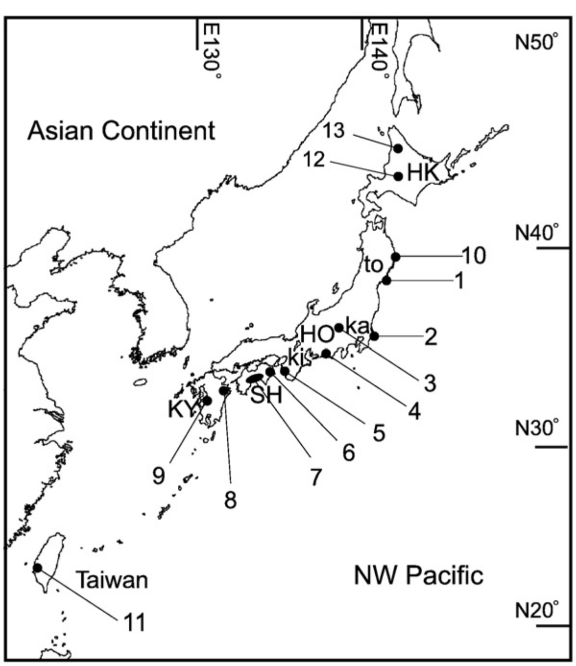

Fig. 1. Occurrences of *Neithea* in the Cretaceous of Northwest Pacific. All locality numbers are compatible with those from Table 1. HK; Hokkaido Island, HO; Honshu Island, SH; Shikoku Island, KY; Kyushu Island, to; Tohoku area, ka; Kanto area, ki; Kinki area.

Table 1
Neithea species reported from the Cretaceous of the Northwest Pacific

Species	Original designation	Biogeographic type of species	Stratigraphic range in Northwest Pacific (in Mediterranean region)	Formation (locality and loc. no.)
N. alta	Hayami in Hayami and Noda (1977)	Endemic	Berriasian	Ayukawa Formation (Tohoku, 1)
N. atava	Roemer (1839)	Widespread	Hauterivian–late Aptian (Beriasian–Albian?)	Kimigahama (Kanto, 2), Ishido (Kanto, 3), Idaira (Kanto, 4), Arida (Kinki, 5), Lower Hanoura, Hanoura (eastern Shikoku,6), Monobe, Lower Monobe (central Shikoku), 7), Haidateyama, Osaka (eastern Kyushu, 8), Sanpozan, Hachiryuzan, Hinagu (western Kyushu, 9) formations
N. hanourensis	Tashiro and Kozai (1986)	Endemic	Barremian	Lower Hanoura Formation (eastern Shikoku, 6)
N. notabilis	Von Münster in Goldfuss (1833)	Widespread	Barremian–late Aptian (Neocomian–Turonian)	Ashikajima, Kimigahama (Kanto, 2), Ishido (Kanto, 3), idaira (Kanto, 7), Hiraiga (Tohoku, 10) formations
N. matsumotoi	Hayami (1965)	Endemic	Barremian–late Albian	"Sebayashi" (Kanto, 3), Doganaro (central Shikoku, 7), Sukubo, Haidateyama (eastern Kyushu, 8) Hachiryuzan, Kesado, (western Kyushu, 9) formations and Upper Aptian of Peikang area (Taiwan, 11)
N. alpina	d'Orbigny (1847)	Widespread	Early–late Aptian (Albian–Maastrichtian)	Hibihara (central Shikoku, 7), Osaka (eastern Kyushu, 8), Tomochi, Imaizumigawa (western Kyushu, 9), Hiragia (Tohoku, 10), Shuparogawa? (central Hokkaido, 12) formations
N. syriaca amanoi	Hayami (1965)	Widespread (see text for detail)	Early Aptian–early Albian (Barremian–Cenomanian = range of *N. syriaca syriaca*)	Ashikajima, Kimigahama (Kanto, 2), Bunjo, Hagino (central Shikoku, 7), Tamarimizu, Osaka (eastern Kyushu, 8), Kesado (western Kyushu, 9), Kamiji (northern Hokkaido, 13) formations
N. nipponica	Hayami (1965)	Endemic	Late Aptian–early Albian	Hiraiga and Aketo formations (Tohoku, 10)
N. "*kochiensis*"	Hayami in Hayami and Kawasawa (1967)	Uncertain taxonomic position (see text for detail)		Doganaro (central Shikoku, 7) and Osaka (eastern Kyushu, 8) formations
N. "*aketoenis*"	Hayami (1965)	Uncertain taxonomic position (see text for detail)		Aketo Formation (Tohoku, 10)

See Appendix for references in each area. All localities are comparable to Fig. 1.

are known exclusively in the Northwest Pacific region, whereas widespread species are those that have been recorded from other regions as well. In addition, the subspecies (*N. syriaca amanoi*) is considered here to be a widespread species.

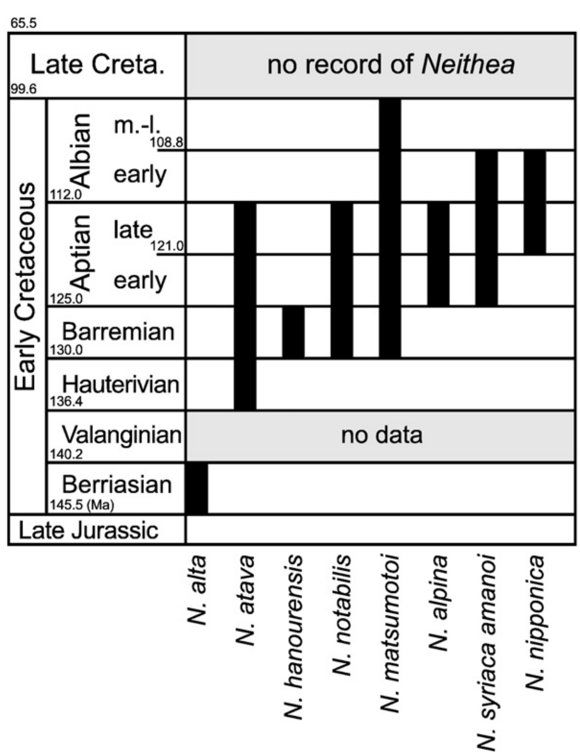

Fig. 2. Stratigraphic ranges of *Neithea* species in the Cretaceous of Northwest Pacific.

4. Results: spatiotemporal changes in *Neithea* species in the Cretaceous Northwest Pacific

Neithea is known from 32 formations in the Northwest Pacific (Fig. 1 and Table 1). Stratigraphic distribution of each species is shown in Fig. 2. The earliest record of *Neithea* in this region is known from the Berriasian, and it occurs almost continuously up into the upper Albian (Fig. 2). We could not obtain any specimens from Valanginian strata because shallow marine deposits of this age have a very restricted distribution in the Northwest Pacific.

Neithea alta, *N. hanourensis*, *N. nipponica*, and *N. matsumotoi* (Fig. 3) are all endemic species, whereas *N. atava*, *N. notabilis*, *N. alpina*, and *N. syriaca* are widespread species (Table 1). Species diversity clearly increased during the Berriasian to late Aptian interval, when it reached a maximum of six species (Fig. 4A). Subsequently, the diversity gradually decreased during the early to late Albian (Fig. 4A). There is no record of *Neithea* in the post-late Albian Cretaceous. Low demise ratios were obtained for the Hauterivian/Barremian (0), Barremian/early Aptian (0.25), and early Aptian/late Aptian (0) boundaries (Fig. 4B). Thereafter demise ratios increased during the late Aptian/early Albian to the middle–late Albian/Cenomanian (0.50, 0.66 and 1 for the late Aptian/early Albian, early Albian/middle–late Albian and middle-late Albian/early Cenomanian, respectively) (Fig. 4B). Origination ratios gradually decreased during the Hauterivian/Barremian to early Aptian/late Aptian (0.75, 0.40, and 0.16 for the Hauterivian/Barremian, Barremian/early Aptian and early Aptian/late Aptian, respectively). In addition, no origination occurred in the late Aptian/early Albian, early Albian/middle-late Albian, and middle-late Albian/early Cenomanian (Fig. 4B). In particular, high demise ratios in the absence of origination are characteristic of the late Aptian/early Albian, early Albian/middle-late Albian, and middle-late Albian/early Cenomanian boundaries (Fig. 4B). The ratio of widespread species gradually decreased during early Aptian to early Albian (80, 66, and 33% for early Aptian, late Aptian,

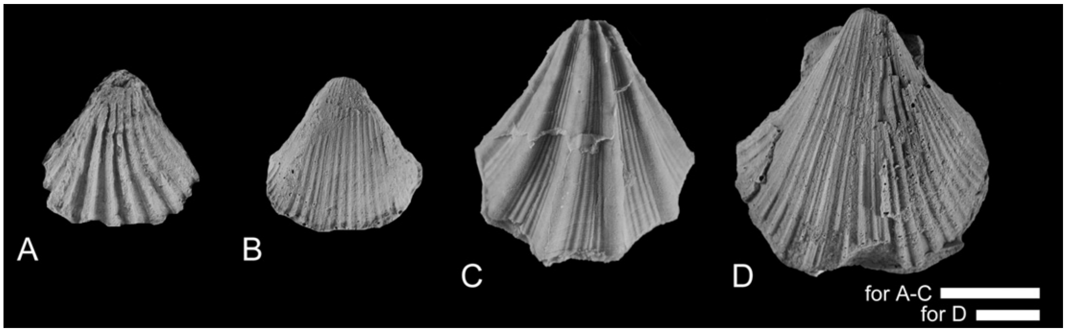

Fig. 3. Endemic species of *Neithea* in the Northwest Pacific. A) *N. alta*. B) *N. hanourensis* C) *N. matsumotoi*. D) *N. nipponica*. A is the holotype, B–D are plaster models of holotypes. All specimens are right valves. Scale-bars are 1 cm.

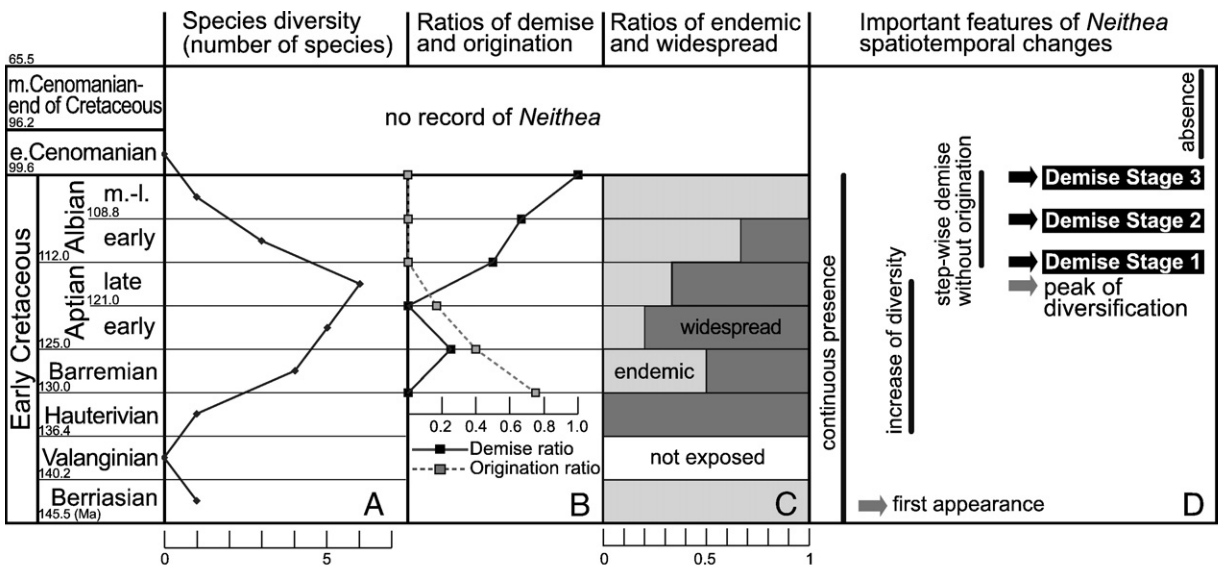

Fig. 4. Spatiotemporal changes of *Neithea* in the Northwest Pacific. A) species diversity changes. B) ratios of demise (DR) and origination (OR) at each stage and/or substage boundary. C) ratios of endemic and widespread species for each stage and/or substage. D) important features of *Neithea* spatiotemporal changes.

and early Albian, respectively), and widespread species were absent in middle-late Albian (Fig. 4C).

5. Discussion

5.1. Diversification phase of Neithea during the Early Cretaceous

Neithea originated in the Berriasian, thrived in the mid-Cretaceous, then decreased in diversity and finally became extinct in the terminal Cretaceous (Dhondt, 1981, 1992). The first appearance of *Neithea* in the Northwest Pacific is virtually synchronous with the earliest occurrences (Berriasian) of *Neithea* in the Tethyan region (Dhondt, 1973). Since its first appearance in the Berriasian, *Neithea* was continuously present until the late Albian in the Northwest Pacific. Iba and Sano (2006, 2007) concluded that tropical–subtropical conditions prevailed in the Northwest Pacific during the Berriasian to Albian, based on spatiotemporal distribution patterns of Mesogean taxa. The continuing presence of *Neithea* in the Northwest Pacific during this interval strongly supports Iba and Sano's (2006, 2007) conclusions. After a period of gradual increase in diversity of *Neithea* species in the Northwest Pacific during the Hauterivian to late Aptian, they reached their maximum diversity in the late Aptian. This coincides with late Aptian northward development of large carbonate platforms, inhabited by diverse Mesogean taxa (Sano, 1995; Iba and Sano, 2006, 2007; Takashima et al., 2007). This northward expansion of carbonate platform distribution in the Northwest Pacific is interpreted by Takashima et al. (2007) as being a consequence of the Late Aptian global warming phase, the Aptian Greenhouse Earth II period determined by Weissert and Lini (1991). The maximum diversity of *Neithea* is most probably related to this Late Aptian warming phase.

5.2. Step-wise demise of Neithea in the Albian of the Northwest Pacific

The Albian demise of *Neithea* in the Northwest Pacific can be subdivided into three stages (Fig. 4D); Stage 1 (late Aptian–early Albian interval), Stage 2 (early Albian to middle–late Albian interval), and Stage 3 (late Albian–early Cenomanian interval). In Stage 1, three widespread species, *N. atava*, *N. notabilis*, and *N. alpina* disappeared. Species diversity started to decrease coincident with no origination and high demise ratios from this stage (Fig. 4). In Stage 2, widespread species disappeared completely and only one species *N. matsumotoi* could survive. In Stage 3, *Neithea* completely disappeared in the Northwest Pacific and never reappeared (Figs. 2 and 4). Although Upper Cretaceous shallow marine deposits containing abundant molluscan fossils such as trigonid and ostreid bivalves are distributed widely in the Northwest Pacific margin (e.g., Komatsu, 1999; Komatsu and Maeda, 2005; Ando, 2003), there have been no reports of *Neithea* in this period. This suggests that the demise of *Neithea* was not the result of facies change and/or lack of Upper Cretaceous marine strata.

In the Northwest Pacific three widespread species, *N. atava*, *N. notabilis*, and *N. alpina*, disappeared in Stage 1 and *N. syriaca* in Stage 2, however, these taxa are known to have been in Tethys sea (e.g., Mediterranean region) until the Albian, Turonian, Maastrichtian, and Cenomanian, respectively (Table 1) (Dhondt, 1973). These lines of evidence illustrate the different stratigraphic ranges of the same species between the Northwest Pacific and Tethyan regions and should therefore been considered as a demise of *Neithea* in the Northwest Pacific, and not the extinction of the species. It indicates that some profound paleoceanographic changes caused the demise of *Neithea* in the Northwest Pacific.

In order to investigate the disparity in temporal change of *Neithea* species diversity between the Northwest Pacific and the Mediterranean region (Fig. 5), available data from Dhondt (1973, 1982, 1985), Dhondt and Dieni (1993), and Perrilliat et al. (2006) is compiled in this study. The data reveals that in the Mediterranean region *Neithea* gradually diversified during the Berriasian to Cenomanian, at which point it reached maximum diversity (15 species), and thereafter species diversity decreased until its extinction in the terminal Cretaceous (Fig. 5). Mid-Cretaceous times are known to be a typical greenhouse period, and a significant warming trend during Late Aptian to Turonian has been reconstructed from oxygen isotopic records (Fig. 5) (e.g., Clarke and Jenkyns, 1999; Wilson and Norris, 2001; Huber et al., 2002; Steuber et al., 2005). The Albian diversification of *Neithea* in the Mediterranean region is consistent with the mid-Cretaceous global warming trend and sea-level rise (Fig. 5). The step-wise demise of *Neithea* during the Albian in the Northwest Pacific is opposite and counterpart to the diversification trend seen in the Mediterranean, and contrary to the mid-Cretaceous global warming trend (Fig. 5). This gradual demise of *Neithea* and its subsequent long-term absence throughout the Late Cretaceous has not been recorded in Mediterranean, Caribbean, or indeed in any other regions of Tethys. Therefore, the biotic change of *Neithea* in the Northwest Pacific was a unique bio-event in this area.

5.3. Paleobiogeographic implications of *Neithea* demise

Contemporaneous and profound long-term biotic changes took place in the Northwest Pacific during the mid-Cretaceous. Iba and Sano (2006, 2007) have analyzed the gradual demise pattern of Mesogean taxa (*sensu* Masse, 1992) in the mid-Cretaceous Northwest Pacific and revealed that Mesogean key reference taxa (rudists and dasyclads) and some Mesogean indicators (hermatypic corals and stromatoporoids) disappeared in the latest Aptian to early Albian interval. Iba and Sano (2007) coined the term “Mesogean key taxa demise event” to describe the simultaneous and gradual disappearance of several taxa. That event was followed by the final disappearance of all Mesogean indicators in the early Albian to middle Albian interval in the Northwest Pacific (“Mesogean indicators demise event” of Iba and Sano, 2007). This step-wise demise of Mesogean taxa clearly indicates that the Northwest Pacific became independent from Tethyan Realm during latest Aptian to middle Albian, and led to the establishment of the North Pacific Province (Iba and Sano, 2007) (Fig. 6).

Stages 1 and 2 of *Neithea* demise are simultaneous with the Mesogean key taxa demise event and Mesogean indicator demise event, respectively. This shows that the step-wise demise of biota in the Northwest Pacific can be recognized not only in Mesogean taxa but

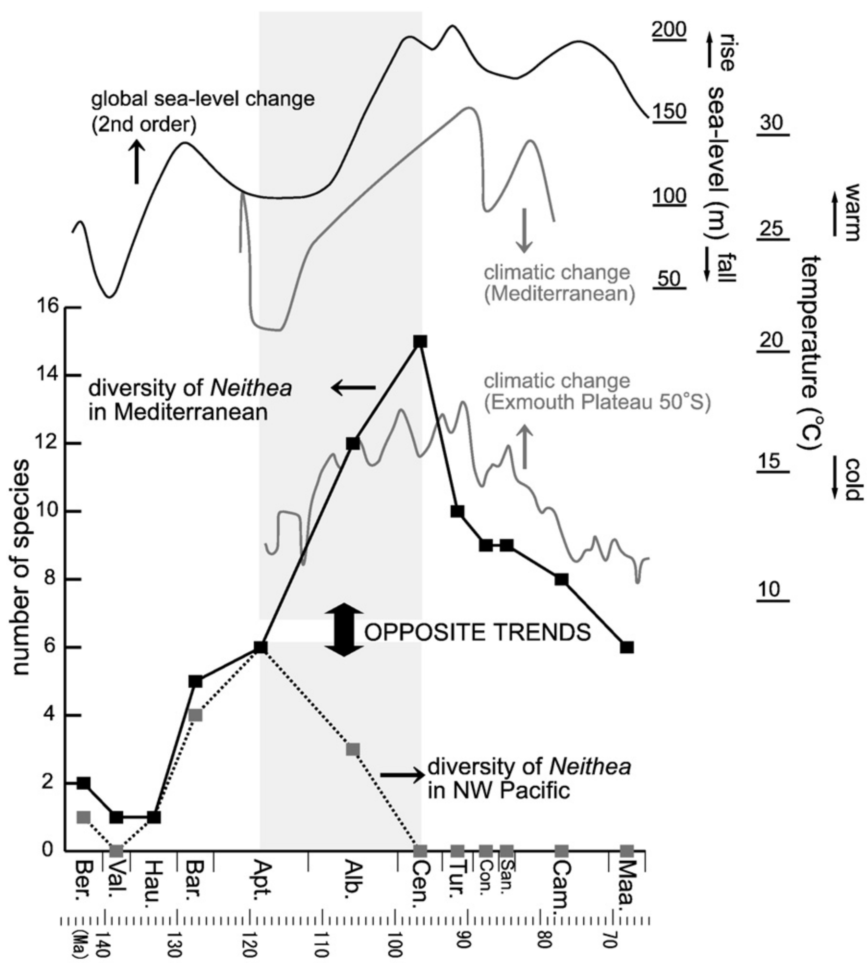

Fig. 5. Graph of *Neithea* species diversity in the Northwest Pacific and the Mediterranean region plotted against Cretaceous global changes in sea-level and climate. Species diversity of *Neithea* in the Mediterranean region compiled from Dhondt (1973, 1982, 1985), Dhondt and Dieni (1993), and Perrilliat et al. (2006). Climatic changes based on Clarke and Jenkyns (1999) (Exmouth Plateau) and Steuber et al. (2005) (Mediterranean). Global sea-level changes based on Hardenbol et al. (1998). Cretaceous time scale based on Ogg et al. (2004).

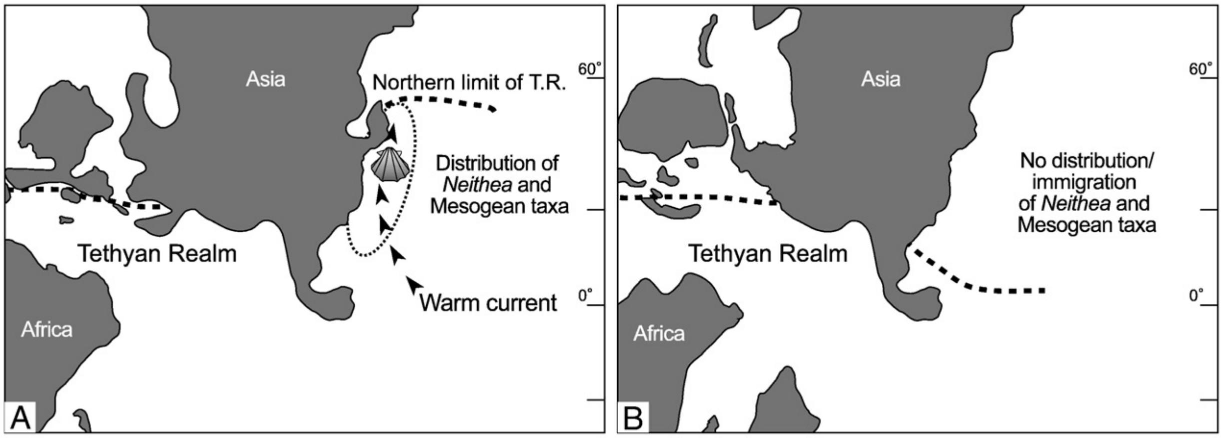

Fig. 6. Illustrating the changes in distribution of *Neithea* and Mesogean taxa, and changing northern limit of the Tethyan Realm in the Cretaceous. A) Early Cretaceous, B) Late Cretaceous. Map for the Early (120 Ma) and Late Cretaceous (80 Ma) based on Barron et al. (1981). Northern limit of the Tethyan Realm in Mediterranean region based on Masse (1992) and Voigt et al. (1999).

also in the Tethyan non-rudist bivalve *Neithea*, though the Albian demise of the *Neithea* (three stages) was more protracted than the demise of Mesogean taxa (two stages).

Demise of widespread species of *Neithea* in Stages 1 and 2 indicate start of a weakening in the faunal connection between the Northwest Pacific and Tethys, whilst the complete demise of *Neithea* in Stage 3 suggests that the faunal connection between the two oceans deteriorated significantly in this stage (Fig. 6). During the mid-Cretaceous warming period, widespread species that disappeared in the Northwest Pacific in Stages 1 and 2 (e.g., *N. atava*, *N. notabilis*), and other widespread species (e.g., *N. hispanica*, *N. sexangularis*, *N. reguraris*) were widely distributed in other oceans (Dhondt, 1973, 1982; Dhondt and Dieni, 1993; Andrade et al., 2004; Perrilliat et al., 2006). However, these widespread species never penetrated and/or re-immigrated into the Northwest Pacific (Fig. 6). Long-term absence of *Neithea* in the Late Cretaceous of the Northwest Pacific could have resulted from restricted faunal interchange between Northwest Pacific and other oceans during that time.

5.4. Possible causes of Neithea demise in the Northwest Pacific

Recently, the early Albian "cooling" episode is recognized in the Northwest Pacific (Iba, in press). A typical Arctic-type ammonite *Arcthoplites* (*Subarcthoplites*) sp. was discovered from the lower Albian of northern Hokkaido, northern Japan (Loc. 13 in Fig. 1). Iba (in press) considered this southward distribution of Arctic-type ammonite as the appearance of a distinct "cooling" episode in the early Albian Northwest Pacific.

Results of some recent climatic model simulations can explain this Albian "cooling" episode in the Northwest Pacific. The Aptian–Albian interval should be paid attention as a time of major changes in paleogeographic/paleoceanographic settings, due to the formation of new oceanic gateways. It has been postulated that the opening of the equatorial Atlantic gateway (EAG) changed not only the adjacent ocean current system, but also those in the Pacific (Poulsen et al., 2003; Poulsen and Huynh, 2006). Recently, Poulsen and Huynh (2006) numerically simulated the conditions of oceanic circulation in the Albian Pacific, paying special attention to the increase in atmospheric CO_2 and opening of the EAG. As a consequence of the EAG opening, the simulation suggested the generation of a relatively cold water mass in the Pacific, contrasting with the Atlantic and Indian Oceans. In addition, an increase in atmospheric CO_2 would strongly weaken the paleo-Kuroshio warm current, a clockwise current flows from south to north along the Northwest Pacific margin (Poulsen and Huynh, 2006). The paleo-Kuroshio warm current was the most important controlling factor for the distribution and immigration of tropical biota in the Northwest Pacific (e.g., Iba and Sano, 2007) (Fig. 6).

These profound Albian "cool" conditions and changes in oceanic circulation/heat transport would affect the demise of Tethyan biota (i.e., Mesogean taxa and *Neithea*) in the Northwest Pacific and also restrict faunal immigration into the Northwest Pacific from the Tethys Sea (Fig. 6). This new hypothesis of paleobiogeography and paleoceanography in the mid-Cretaceous Northwest Pacific warrants verification and further research.

6. Conclusions

1. *Neithea* was continuously distributed in the Northwest Pacific during the Berriasian to late Albian, suggesting that the Northwest Pacific was not distinct biogeographically from the Tethyan Realm during this time interval. During the Hauterivian to late Aptian, the Northwest Pacific species diversity of *Neithea* increased gradually with a low demise rate and a high origination rate, reaching a maximum in the late Aptian. This most probably occurred in con`-junction with the global warming phase at that time.
2. The step-wise demise of *Neithea* in the Northwest Pacific is recognized and subdivided into three stages: at the late Aptian–early Albian interval (Stage 1), early Albian to middle–late Albian interval (Stage 2), and in the late Albian–early Cenomanian (Stage 3). Following the Albian, *Neithea* disappeared in the Northwest Pacific and never reappeared. This pattern is unique to the Northwest Pacific as it has not been recorded from any other regions of Tethyan Realm. This pattern is the reverse of the Albian diversification of *Neithea* in the Mediterranean region and Mid-Cretaceous global warming trend.
3. Stages 1 and 2 of *Neithea* demise coincide in timing with the Mesogean key taxa demise event and Mesogean indicator demise event (*sensu* Iba and Sano, 2007), respectively. Gradual demise of *Neithea* during the Albian and its subsequent absence in the Northwest Pacific strongly supports the idea that the independence of the North Pacific Province from the Tethyan Realm was gradual, and possibly caused by long-term deterioration of the faunal interchange. This deterioration of faunal interchange could be explained by Albian "cooling" conditions and changes in oceanic circulation/heat transport in the Northwest Pacific.

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Appendix A. List of literature surveyed to elucidate the stratigraphic distribution of *Neithea* in this study

Hokkaido Island

Hayami, T., Noda, M., 1977. Note on the morphology of *Neithea* (Cretaceous pectinids) with taxonomic revision of Japanese species. Transaction and Proceedings of the Palaeontological Society of Japan, new series 105, 27–54.

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Honshu Island (Tohoku, Kanto and Kinki areas)

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