

Comparison of the geographical and stratigraphical ranges of Fortipectininae and Patinopectininae (Bivalvia : Pectinidae)

Alexander I. Kafanov*

Fortipectininae と Patinopectininae の地理的・層序的分布の比較

アレキサンダー, I. カヴァノフ*

(Abstract)

The history of studies of Fortipectininae Masuda, 1963 and Patinopectininae Habe, 1977, the size and composition of the subfamilies and their systematic relationships are considered. It is concluded that Fortipectininae is a typical group of near-Asian Pacific origin, and it has been in North Japan-Sakhalin Paleogene province in the Late Oligocene. Some members of this subfamily - species of the genera *Mizuhopecten* and *Fortipecten* migrated to the American coast of the North Pacific in the Late Miocene and Early Pliocene. The Patinopectininae is a group of Neogene genesis, forming and further evolution of this group are wholly connected with the Pacific coast of North America.

Patinopecten has never spread to the North-West Pacific. An analysis of phylogenetical and geochronological relationships of the two subfamilies gives an additional and quite important argument for regarding the *Mizuhopecten* (Fortipectininae) and the *Patinopecten* (Patinopectininae) as two separate genera with independent phylogenetic development.

(要 旨)

軟体動物二枚貝類 Pectinidae 科の Fortipectininae Masuda, 1963 と Patinopectininae Habe, 1977 両亜科の研究史, 構成属・種の時空分布及びそれらの系統分類学的問題について検討・考察を行った。その結果, 次のことが明らかとなった。Fortipectininae 亜科は, 後期漸新世に北日本-樺太地域で発生した典型的なアジア-太平洋起源のグループである。この亜科の *Mizuhopecten* と *Fortipecten* 属の数は, 後期中新世と初期鮮新世にそれぞれ北太平洋アメリカ合衆国西海岸域に移動している。これに対して, Patinopectininae 亜科は, 新第三紀起源のグループで, 北米アメリカ太平洋沿岸で発生し, 繁栄・進化したものである。*Patinopecten* 属は北西太平洋域には全くその分布を広げたことはない。

* Laboratory of Ecosystem Dynamics, Institute of Marine Biology, Far Eastern Science Center, USSR Academy of Sciences, Vladivostok, 690022, USSR.

(ソ連科学アカデミー, 極東科学センター, 海洋生物研究所生態系研究部門)

即ち、Fortipectininae 亜科の *Mizuhopecten* と Patinopectininae 亜科の *Patinopecten* は各々、独立した生物地理区を有し進化したものである。 (編者訳)

I Introduction

Among Cenozoic bivalve molluscs of the North Pacific, pectinids of the subfamily Fortipectininae (Masuda, 1963) are the most interesting group. The large and strong shells are well preserved as fossils, and their broad geographical and geochronological distributions are responsible for the important role of Fortipectininae in paleobiogeographic reconstructions and in wide submeridional and sublatitudinal biostratigraphic correlation of Paleogene and Neogene deposits of the northern Pacific mobile belt.

However, the systematics of the subfamily has not yet been finalized. Although the majority of Soviet, Japanese and American paleontologists accept the validity of the genus *Mizuhopecten* Masuda, 1963 and distinguish it from the genus *Patinopecten* Dall (1898), zoologists have not yet come to any common opinion. In particular, "*Pecten*" *yessoensis* Jay, 1856, one of the most important commercial invertebrates and an object of fishery and mariculture in the Soviet Far East and in Japan, is cited in zoological literature as *Pecten* (*Patinopecten*) (Scarlato, 1960), *Patinopecten* (Yamamoto and Habe, 1958; Kira, 1960; Golikov and Scarlato, 1967) or *Patinopecten* (*Mizuhopecten*) (Habe and Ito, 1965; Habe and Kosuge, 1967; Habe, 1977; Scarlato, 1981).

II Historical review

For an analysis of the taxonomic position of the subfamily Fortipectininae and of taxonomic relationships between the genera *Mizuhopecten* and *Patinopecten*, it is reasonable not only to use morphological characteristics, but also to consider the phylogenetic and geochronological relationships of the group and of other related taxa.

The genus *Patinopecten* Dall (1898, p. 695)* was established by Dall as a section of the genus *Pecten* Müller (1776, p. 248) with type-species (by original designation) *Pecten caurinus* Gould (1850, p. 345). This species is known as fossil in the Pliocene, and inhabits the Recent shelf (10–200m depths) in British Columbia, Washington, Oregon and California, from 36° to 59° N (Bernard, 1983). Besides the type-species, the group of typical American *Patinopecten* species includes a number of Neogene species: *P. coosensis* (Shumard, 1858) from Pliocene deposits of Coos Bay, Oregon; *P. haywardensis* Lutz, 1951 and *P. haywardensis calaverasensis* Hall, 1958 from Middle-Miocene deposits of California; *P. merriami* (Arnold, 1906) from the Pliocene Piko Formation of California; *P. oregonensis* (Howe, 1922) described from the Upper Miocene Empire Formation of Oregon, and a zonal

* *Philippia* (*Blanckenhornia*) von Teppner (1922, p. 87, 260, with type-species *Pecten* (*Patinopecten*) *lohri* Hertlein, 1928 (nom. nov. pro *Pecten* (*Patinopecten*) *oweni* Arnold, 1906 non *Pecten oweni* de Gregorio, 1884) is a synonym of *Patinopecten*.

species of the Wishkahan Stage (Addicott, 1976) of the Northwestern states of the U.S.A. and of British Columbia; *P. oregonensis cancellosus* Moore (1963) from the Miocene of Coos Bay, Oregon; *P. propatulus* (Conrad, 1849) described from the Middle Miocene Astoria and Tumbler formations of Washington and California, and a zonal species of the Newportian Stage (Addicott, 1976) of the Northwestern stages of the U.S.A. and of British Columbia; *P. skonunensis* MacNeil (1967) from the Miocene Skonun Formation of the Queen Charlotte Isles, British Columbia.

MacNeil (1961, p. 227) established a new subgenus *Patinopecten* (*Lituyapecten*) and included in it: *P. (L.) dilleri* (Dall, 1901) from Pliocene deposits of California and, probably, from Upper Miocene (?) and/or Lower Pliocene formations of the Lituya Bay area, Alaska (a zonal species of the Moclipsian Stage (Addicott, 1976), of the Northwestern states of the U.S.A. and of British Columbia); *P. (L.) falorensis* MacNeil (1961) from the Pliocene Falor, Rio-Dell and Purisima formations of California; *P. (L.) jonesi* Kanno (1971) from Middle Miocene deposits of the northern coasts of the Gulf of Alaska; *P. (L.) purisimaensis* Arnold (1906) from the Pliocene Purisima Formation of the Central California; *P. (L.) yakatagensis* (Clark, 1932) from Lower and Middle Miocene deposits of the northern coast of the Gulf of Alaska.

Moreover, a group of "split-ribbed" patinopectens has been distinguished (Addicott, 1974): *P. healeyi* Arnold, 1906 from the Pliocene Piko Formation of California and *P. lohri* Hertlein, 1928 from Pliocene deposits of the Santa Barbara district, California. Addicott (1974) believed that this group probably requires the establishment of a separate subgenus.

For the common scallop living Japanese "*Pecten*" *yessoensis*, the generic name *Patinopecten* was probably used for the first time by Kuroda (1932). The name was also applied later to morphologically similar fossil forms. At least 23 valid species group taxa were united under the generic name *Patinopecten* in the fundamental work of Masuda (1962). However, Masuda (1962) was the first to note that Asian and American "*Patinopecten*" species differ considerably in the details of their radial ribbing, in the structure of their auricles and, presumably, in the structure of the pseudo-hinge apparatus. This led him to establish for Asian "*Patinopecten*" the new genus *Mizuhopecten* Masuda (1963, p. 151) with type species *Pecten yessoensis* Jay, 1856.

True *Patinopecten* is distinguishable from *Mizuhopecten* by its smaller auricles, of which the anterior one of the right valve has a deep byssal notch; by having a smaller posterior auricle as compared to the anterior auricle in the left valve; by its distinct, elongate auricular crura, well distinguished in juvenile specimens, but smoothed away with ageing; by its faintly developed lateral elongate elevation; by having a double distal tooth of the posterior crura on the left valve and by the distal tooth being distinctly developed; by having a flattened right valve; by its flattened and angular radial ribs on the right valve and topped ribs on the the left valve (*Mizuhopecten* species have rounded ribs on both the right and left valves, the left valve often having a fine reticulation; and by its intercostal

spaces being narrower than or almost to the width of the ribs on the right valve). These differences are constant and indicate a clear morphological distinction between these two groups.

Grau (1959) included in the genus *Pecten* two separate subgenera, *Patinopecten* and *Oppenheimopecten* von Teppner (1922, p. 254). Masuda (1962), a prominent specialist in the systematics of Paleogene-Neogene Pectinidae of the North Pacific, in his review of pectinids of Japan, treated the Asian "*Patinopecten* s.s." together with *Pecten* (*Fortipecten*) Yabe and Hatai (1940, p. 149) and *Patinopecten* (*Kotorapecten*) Masuda (1962, p. 216) as subgenera of the genus *Patinopecten* Dall (1898) and included the latter together with *Pecten* Müller, 1776 in the subfamily Pectininae "Lamarck, 1819". Also, Masuda (1962) described the subgenus *Placopecten* (*Nipponopecten*) Masuda (1962, p. 194) within "Chlamiinae n. subfam." (= Chlamydiae Korobkov, 1957) and later Masuda (1963) likened it to *Mizuhopecten*.

Akiyama (1962) published his review of Japanese "*Patinopecten*" somewhat before that of Masuda's (1962) review. Akiyama (1962) separated the genus *Patinopecten* into subgenera *Patinopecten* s.s., including also American forms, and *Patinopecten* (*Masudapecten*) Akiyama (1962, p. 107). The genus *Fortipecten* was treated by Akiyama as a synonym of *Patinopecten* s.s.; Akiyama (*op. cit.*) believed that the type species of the genus, *Pecten takahashii* Yokoyama, 1930, is a descendant of *P. murayamai murayamai* (Yokoyama, 1926) (= *Mizuhopecten kimurai murayamai*), which became adapted to the specific conditions of shore lagoons and acquired a very thick and convex shell. This opinion seems to be wrong and is not shared now by other specialists.

Masuda (1963), studying the problem of the so-called "*Patinopecten*" species of Japan, came to conclusion that it was necessary to establish a new subfamily Fortipectininae Masuda (1963, p. 149), in which the author included *Fortipecten*, *Mizuhopecten*, *Kotorapecten*, *Nipponopecten*, and *Masudapecten*. In this connection, MacNeil (1967, p. 42-43) wrote: "*Fortipecten* is characterized by a very large adductor muscle, and in this character alone it is very distinct from *Patinopecten*. It is equally distinct on this basis from the other Japanese genera, *Masudapecten*, *Kotorapecten*, *Mizuhopecten* and *Nipponopecten*, that Masuda included in the Fortipectininae. I am not convinced that *Masudapecten*, *Kotorapecten*, and *Mizuhopecten* are sufficiently removed from *Patinopecten* to be included in a different subfamily. If a subfamily name is required, I would prefer to place these four genera in a subfamily Patinopectininae. *Fortipecten* is so unique that, pending further knowledge of its ancestry, it could stand in a subfamily of its own. Fortipectininae would, of course, have priority as a subfamily name for the group of *Fortipecten*". This opinion of MacNeil is poorly substantiated, because in taxonomic studies of pectinids MacNeil did not use the characteristics of the structures of the pseudo-hinge apparatus, an important complex of characteristics in the systematics of the group. No doubt, the genus *Patinopecten* should be considered apart from Fortipectininae. However, the name Patinopectininae proposed

informally by MacNeil does not seem to be valid.

Habe (1977, p. 91), in his review of Japanese Bivalvia and Scaphopoda, gave by mistake a diagnosis (in Japanese) of the subfamily Patinopectininae "Masuda, 1962"*, in which he included the genus *Patinopecten*, with subgenera *Patinopecten* s.s., *Mizuhopecten*, *Yabepecten* Masuda (1963, p. 149), and *Kotorapecten*, and the genus *Fortipecten*. Thus, according to International Code of Zoological Nomenclature, Habe is the author of the subfamily Patinopectininae Habe, 1977. This subfamily contains only *Patinopecten* s.s., *Patinopecten* (*Lituyapecten*), "split-ribbed" *Patinopecten* species and, probably, *Vertipecten* Grant and Gale (1931, p. 188). The taxonomic position of the genus *Yabepecten* still remains unclear, but, at least it is clear that the genus does not belong to either Fortipectininae or Patinopectininae.

III Revision of Fortipectininae

The classification and contents of the subfamily Fortipectininae adopted in the present paper is as follows**:

Family Pectinidae Rafinesque, 1815

Subfamily Fortipectininae Masuda, 1963

Genus *Fortipecten* Yabe and Hatai, 1940

F. hallae (Dall, 1921) (= *Pecten* (*Patinopecten*) *rhytidus* Dall, 1921); Beringian and Anvilian strata of Alaska, Ustj-Limimteveyamskaya suite of Karaginsky Island, Eastern Kamchatka; Upper Pliocene.

F. kenyoshiensis Chinzei, 1960; Togawa Formation of Aomori Prefecture, Honshu; Enemetskaya suite of Western Kamchatka; Lower Pliocene.

F. kuroishiensis Kotaka and Noda, 1967; Ogawara Formation of Aomori Prefecture, Honshu; Middle Miocene.

F. makarovi Krishtofovich, 1964; upper part of Maruyamaskaya suite, Sakhalin; Lower Pliocene.

F. mironovi (Khomenko, 1934); Pomyrskaya suite of Northern Sakhalin; Lower Pliocene.

F. sachalinensis (Ilyina, 1957); upper part of Maruyamaskaya and lower part of Nutovskaya suites of Sakhalin; Lower Pliocene.

F. takahachiformis Salin, 1964; Ustj-Kamchatskaya series of Eastern Kamchatka; Miocene.

F. takahashii (Yokoyama, 1930) (*Pecten agnatus* Yokoyama, 1930 and *Pecten piltunensis* Khomenko, 1931); Ishiguma, Omori, Motohata, Yushima, Togawa, Tatsunokuchi, Goban-shoyama, Yamada, and Kogota formations of Honshu; Takikawa, Honbetsu, Atsuga,

* Habe makes the same mistake also in his work of 1981. Moreover, the author gives *Pecten tokyoensis* Tokunaga, 1906 as the type species of the subgenus *Patinopecten* (*Mizuhopecten*).

** A complete catalogue of all known taxa of Fortipectininae is given in a separate paper (Kafanov, in press).

Yuchi, Muroan, Horokura, Porokaoshirarike, Mochikubetsu, Kotan and Kushiro formations of Hokkaido; 3rd horizon of Maruyamaskaya suite, lower part of Nutovskaya and Pomyrskaya suites of Sakhalin; Enemtenskaya suite of Western Kamchatka; and lowest part of Shchapinskaya suite of Central Kamchatka; all Lower Pliocene.

Genus *Mizuhopecten* Masuda, 1963

- M. chichibuensis* (Kanno, 1957); Nenokami Sand of Saitama Prefecture, Honshu; Upper Oligocene.
- M. hashimotoi* (Akiyama, 1962); Nakatombetsu Formation of Hokkaido; Upper Miocene.
- M. ibaragiensis* (Masuda, 1953); Hitachi, Kume and Futaba-Tomioka formations of Honshu; Lower Pliocene.
- M. imamurai* (Masuda, 1959); Kawai Formation of Shimane Prefecture, Honshu; Lower Miocene.
- M. kanbaraensis* (Otuka, 1938); Shiroyama Formation of Shizuoka Prefecture, Honshu; Upper Miocene.
- M. kavranensis* Sinelnikova, 1975; Kakertskaya suite of Western Kamchatka; lower part of Middle Miocene.
- M. kimurai* (Yokoyama, 1925); Kokozura and middle part of Kadonosawa formations of Honshu, Tsurikake Formation of Hokkaido; Middle Miocene.
- M. kimurai kagaensis* Ogasawara, 1976; Saikawa Formation of Ishikawa Prefecture, Honshu; Middle Miocene.
- M. kimurai murayamai* (Yokoyama, 1976) (= *Patinopecten hayashii* Kanno, 1957, *P. shibaharensis* Kanno, 1957, and *P. (P.) murayamai bisecta* Akiyama, 1962); Sugota, Shunetzaka, Oisawa, Tanosawa, Yagen, Orito, Nagura, Futatsugoya, Gyonindaki, Hamada, Higashi-Innai and Kurosedani formations of Honshu; Taishu Formation of Kyushu; Heiroku Formation of North Korea; all Lower Miocene.
- M. kimurai nakosoensis* (Masuda, 1960); Kokozura, upper part of the Kadonosawa, Suenomatsuyama, Takahoko and Tomari formations of Honshu; Middle Miocene.
- M. kimurai tiganouraensis* (Nakamura, 1940); Ajiri and Higashi-Innai formations of Honshu; Lower Miocene.
- M. kimurai ugoensis* (Hatai and Nisiyama, 1939); Sugota, Tanosawa and Shunetzaka formations of Honshu, Chikubetsu Formation of Hokkaido; Lower Miocene.
- M. kimurai yudaensis* (Masuda, 1960); Kadonosawa Formation (Shiratori Member) of Iwate Prefecture, Honshu; Lower Miocene.
- M. kitamiensis* Uozumi, Fujie and Matsui, 1966; Ainonai Formation of Hokkaido; Miocene.
- M. kobyamai* (Kamada, 1954); Kabeya and Nakayama formations of Fukushima Prefecture, Honshu; Noya and (?) Chirai formations of Hokkaido; Lower to Middle (?) Miocene.
- M. kudoii* (Nomura, 1935); Tanosawa Formation of Aomori Prefecture, Honshu; Lower Miocene.

- M. kulkensis* (Slodkewitsch, 1938); Etolonskaya suite of Western Kamchatka; Middle and (?) Upper Miocene.
- M. matschiensis* (Krishtofovich, 1964); Sertunajskaya suite of Sakhalin; lower part of Middle Miocene.
- M. matumoriensis* (Nakamura, 1940); Aoso and Nanakita formations of Miyagi Prefecture, Honshu; Middle Miocene.
- M. mitsuganoensis* Shibata, 1970; Ago Sand of Mie Prefecture, Honshu; lower part of Middle Miocene.
- M. mollerensis* (MacNeil, 1967); Bear Lake Formation of Alaska Peninsula; Upper Miocene.
- M. naganoensis* (Masuda, 1962); Shigarami Formation of Nagano Prefecture, Honshu; Lower Pliocene.
- M. nakatombetsuensis* (Akiyama, 1962) (= *Patinopecten (Patinopecten) yessoensis nakatombetsuensis* Masuda, 1962); Nakatombetsu Formation of Hokkaido; Upper Miocene.
- M. ninohensis* (Masuda, 1954); Suenomatsuyama Formation of Iwate Prefecture, Honshu; Middle Miocene.
- M. paraplebejus* (Nomura and Hatai, 1936); Kubota, Urushikubo, Ogane, Kanomatazawa, Otsutsumi, Nanakita and Ginzan formations of Honshu; Middle Miocene.
- M. planicostulatus* (Nomura and Niino, 1932); Shirahama and Kurotaki formations of Honshu; Lower Pliocene.
- M. poculum* (Yokoyama, 1926) (= *Pecten kurosawaensis* Yokoyama, 1926); Sawane, Nishiyama, Sasaoka, Narusawa, Higashimeya, Daishaka, Yamada and Odaira formations of northern Honshu; Yuchi and Sarabetsu formations of Hokkaido; all Lower Pliocene.
- M. poculum tsudae* (Noda, 1962); Higashigawa Formation of Niigata Prefecture, Honshu; middle part of Pliocene.
- M. sannohensis* (Chinzei, 1961); Togawa Formation of Iwate Prefecture, Honshu; Lower Pliocene.
- M. singularis* (Slodkewitsch, 1938); Kakertskaya suite of Western Kamchatka; lower part of Middle Miocene.
- M. slodkewitschi* Sinelnikova, 1969; Etolonskaya suite of Western Kamchatka; Middle and (?) Upper Miocene.
- M. subrefugionensis* (Slodkewitsch, 1938); Kakertskaya suite of Western Kamchatka; lower part of Middle Miocene.
- M. subsingularis* (Sinelnikova, 1975); Etolonskaya suite of Western Kamchatka; Middle and (?) Upper Miocene.
- M. subyessoensis* (Yokoyama, 1930); Kurasijskaya suite of Sakhalin; lower part of Middle Miocene.
- M. togeshitensis* (Akiyama, 1962); Togeshita and Onishika formations of Hokkaido; Lower Pliocene and (?) Upper Miocene.

- M. tokyoensis* (Tokunaga, 1906); Shibikawa, Naganuma, Miyata, Umegase, Sanuki, Sasage, Otadai, Semata, Katori, Tokyo, Nekoya, and upper part of Kakegawa formations of eastern Honshu; Unoki Formation of southern Kyushu; and upper part of Setana Formation of Hokkaido; Upper Pliocene and Lower Pleistocene.
- M. tokyoensis hokurikuensis* (Akiyama, 1962); Omma, Himi, Hamada, Sawane, Koshiha and Nakazato (?) formations of Honshu; Takanabe Formation of southern Kyushu; Pliocene to Lower Pleistocene.
- M. tokyoensis sematensis* (Akiyama, 1962); Semata Formation of Chiba Prefecture, Honshu; Middle Pleistocene.
- M. tryblium* (Yokoyama, 1925); Shigarami Formation of Nagano Prefecture, Honshu; Lower Pliocene.
- M. tryblium shinshuensis* (Akiyama, 1962); Ogikubo Sand of Nagano Prefecture, Honshu; Lower Pliocene.
- M. warreni* Masuda, 1971; Montesano Formation of Washington; Upper Miocene.
- M. yamasakii* (Yokoyama, 1925); Shigarami, Awano (?) and Tsuma formations of Honshu; Lower Pliocene.
- M. yessoensis* (Jay, 1856) (= *Pecten brandtii* Schrenck, 1862); Dainenji, Koshiha, Sawane, Nishiyama, Haizume, Shibikawa and Sasaoka formations of Honshu; Setana, Shishinai and Kushiro formations of Hokkaido; Enemtsenskaya suite of Western Kamchatka; Lower Pliocene to Recent (for Recent distribution see: Scarlato, 1981).
- M. yessoensis pseudoyessoensis* (Akiyama and Miyajima, 1960); Nozima and Koshiha formations of Honshu; Lower Pliocene.
- M. yokoyamae* (Masuda, 1962); Omma, Sawane, Haizume, Nishiyama, Sasaoka, Narusawa and Hamada formations of Honshu; Tomikawa and Setana formations of Hokkaido; Golovninskaya and Parusnaya suites of Kunashir and Iturup Islands of Kuril Islands; all Lower Pliocene.

Genus *Kotorapecten* Masuda, 1962

- K. egregius* (Itoigawa, 1955); Kubohara, Akeyo, Kaya and Kaisekizan formations of Honshu; Lower Miocene.
- K. kagamianus* (Yokoyama, 1923) (= *Pecten plicicosulatus* Matsumoto, 1930); Kimachi, Fujina, Hatatate (Moniwa Member) and Nanao formations of Honshu; Imagane Formation of Hokkaido; Lower and Middle Miocene.
- K. kagamianus moniwaensis* (Masuda, 1958); Moniwa Member, Nanao, Yanagawa and Gyonindai formations of Honshu; Lower Miocene.
- K. kagamianus nimaensis* (Masuda, 1958); Kawai and Tamatsukuri formations of Honshu; Lower Miocene.
- K. kagamianus permirus* (Yokoyama, 1926); Nanao, Oido and Kadonosawa formations of Honshu; Lower Miocene.
- ? *K. korfiensis* Sinelnikova, 1975; "Yaponskich Kamnej" suite of eastern Kamchatka;

Middle (?) Miocene.

K. nakajimai (Masuda, 1954); Hatatate Formation (Moniwa Member) of Miyagi Prefecture, Honshu; Lower Miocene.

Genus *Masudapecten* Akiyama, 1962

M. iwasakiensis (Nomura, 1935) (= *Pecten* (*Lyropecten* ?) *shataii* Nomura, 1935); Tanosawa, Sugota and Yoshino formations of Honshu; Lower Miocene.

M. kintaichiensis (Masuda, 1958); Suenomatsuyama Formation of Iwate Prefecture, Honshu; Middle Miocene.

M. masudai Akiyama, 1962; Sugota Formation of Akita Prefecture, Honshu; Lower Miocene.

Genus *Nipponopecten* Masuda, 1962

N. akihoensis (Matsumoto, 1930); Moniwa, Oido, Nanao and Kobana formations of Honshu; Lower Miocene.

N. wakuyaensis (Masuda, 1956); Oido and Imagane formations of Honshu and Hokkaido; Lower Miocene.

IV Phylogeny and biogeography

It has been shown above that the subfamily Fortipectininae Masuda, 1963, composed of five genera—*Fortipecten* Yabe and Hatai, 1940, *Mizuhopecten* Masuda, 1963, *Kotorapecten* Masuda, 1962, *Masudapecten* Akiyama, 1962, and *Nipponopecten* Masuda, 1962 is a morphologically isolated group, different from the true American *Patinopecten* Dall, 1898 and from other closely related genera included in the subfamily Patinopectininae Habe, 1977. This conclusion is wholly corroborated by phylogenetic, paleontologic and historical-biogeographical evidences.

The most ancient Fortipectininae belong to the genus *Mizuhopecten*, which lasted till the Recent; the single Recent species is *M. yessoensis*. The early stages of the geological history of Fortipectininae are recorded by *M. chichibuensis*, described from the Upper Oligocene Nenokami Sandstone in central Honshu. The species is the only known Paleogene representative of the subfamily. *Mizuhopecten* probably originated from a species of *Chlamys* Röding, 1798. In addition to certain morphological similarities, this suggestion is based on some biological peculiarities of the juvenile stages of *Chlamys* and *Mizuhopecten* (Akiyama, 1962).

A marked increase in species diversity in

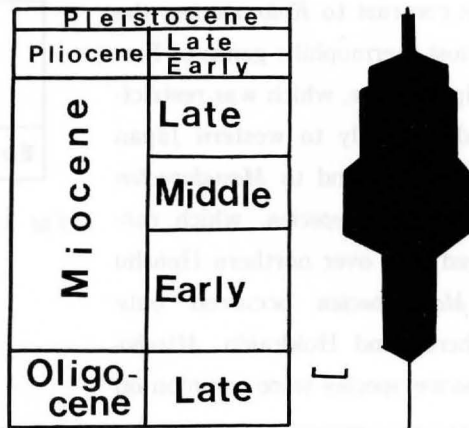


Fig. 1. Changes in *Mizuhopecten* species diversity during the Cenozoic. The scale is equal to 4 species.

Mizuhopecten is observed during the Neogene (Fig. 1). For example, a considerable development is recorded for *M. kimurai*, which evolved a number of geographically and geochronologically vicarious subspecies: Early Miocene *M. kimurai murayamai* from northwestern Kyushu, Honshu and North Korea, *M. kimurai kagaensis* from western Honshu, and *M. kimurai tiganouraensis* from northeastern Honshu; the Middle Miocene *M. kimurai kimurai* from Honshu and Hokkaido, and the Middle and Upper Miocene *M. kimurai nakosoensis* from Honshu. During the early Neogene the genus *Mizuhopecten* spread all over the Japanese Islands (except Hokkaido) and northeastern Korea (Fig. 2).

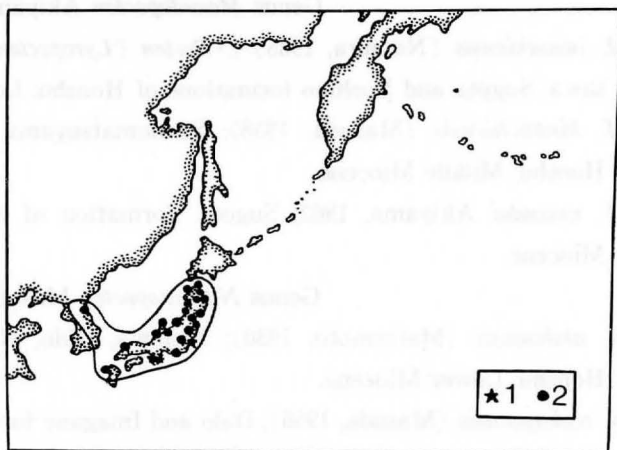


Fig. 2. Geographical and geological distribution of *Mizuhopecten* species during the Late Oligocene (1) and Early Miocene (2). The Early Miocene range of the genus is shown by the line.

An intense diversification of Fortipectininae (Fig. 3) occurred during the early Miocene, leading to the establishment of *Kotorapecten*, *Masudapecten* and *Nipponopecten*; the last is restricted to the Early Miocene. In contrast to *Kotorapecten*, the most thermophilic genus of Fortipectininae, which was restricted generally to western Japan (Fig. 4)*, and to *Masudapecten* and *Nipponopecten*, which ranged only over northern Honshu (*Masudapecten* occurred only there) and Hokkaido, *Mizuhopecten* species were common on

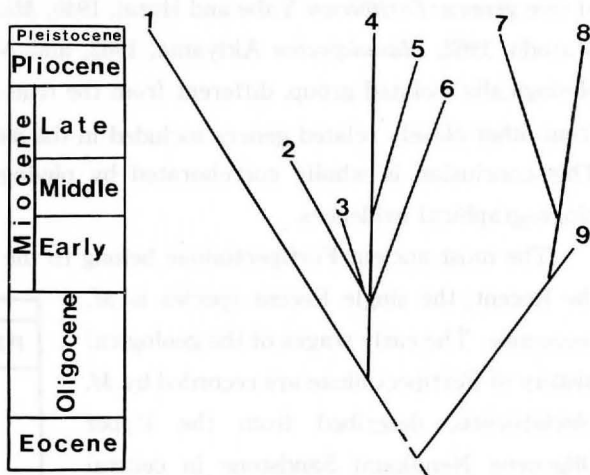


Fig. 3. Proposed relationships between the Fortipectininae (2-6) and Patinopectininae (7-9). 1. *Chlamys* s. l., 2. *Kotorapecten*, 3. *Nipponopecten*, 4. *Mizuhopecten*, 5. *Fortipecten*, 6. *Masudapecten*, 7. *Patinopecten* s.s., 8. *Patinopecten* (*Lituyapecten*), 9. *Vertipecten*.

* The inclusion of *K. korfiensis* Sinelnikova, 1975 in the genus *Kotorapecten* is not conclusively demonstrated, therefore it remains problematical whether the northern limit of the Middle Miocene range of the genus includes Eastern Kamchatka.

both the Japan Sea and the Pacific coasts of Japan (Fig. 2).

During the Middle Miocene, *Mizuhopecten* spread northwards to Hokkaido, Sakhalin and Western Kamchatka (Fig. 5). On the other hand, the area occupied by the genus decreased in the south to include only the northeastern half of Honshu. During the Middle Miocene the diversity of *Mizuhopecten* reached its maximum (Fig. 1), *Fortipecten* isolated from it, and the ancestral form of *Fortipecten* seems to have been *M. matumoriensis* (Masuda, 1956, 1962; Akiyama, 1962; Kotaka and Noda, 1967). By the end of the Middle Miocene the few representatives of the genus *Kotorapecten* became extinct.

The late Miocene is the most interesting period in the geological history of Fortipectininae, and of *Mizuhopecten* in particular. In spite of some decrease in the diversity of *Mizuhopecten* species (Fig. 1), they reached their maximum range, spreading to the eastern part of the North Pacific (Fig. 5). This is well documented by *M. mollerensis*, found in Upper Miocene (?) Bear Lake Formation of the southern shore

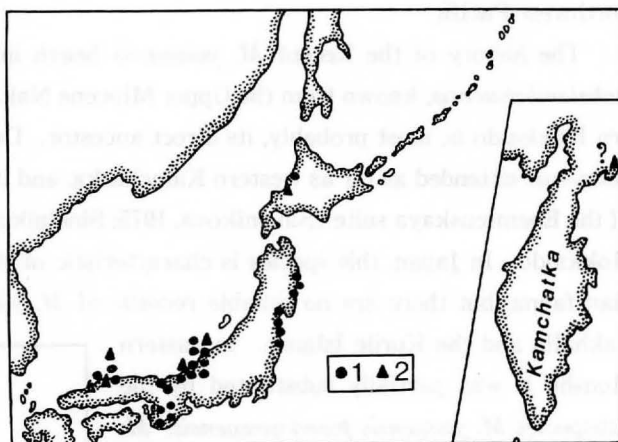


Fig. 4. Geographical and geological distribution of *Kotorapecten* species during the Early (1) and Middle (2) Miocene.

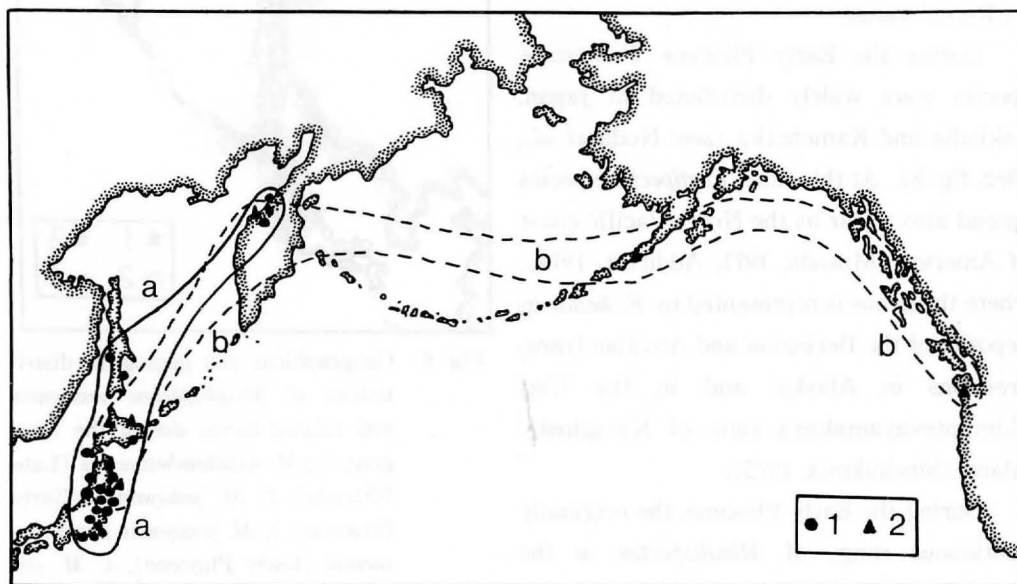


Fig. 5. Geographical and geological distribution of *Mizuhopecten* species during the Middle (1) and Late (2) Miocene. The range limits: a; Middle Miocene, b; Late Miocene.

of Port Moller Bay, Alaskan Peninsula, and by *M. warreni* from the Upper Miocene Montesano Formation of Washington.

In addition to *Mizuhopecten*, representatives of the genus *Yabepecten* extended at the same time as far as the Pacific coast of North America (Masuda, 1977, 1978). Hence, *Y. alaskensis* (MacNeil, 1967) occurs in Lower Pliocene deposits of the Malaspina district, Alaska, and *Y. condoni* (Hertlein, 1925) is a zonal species of the Graysian Stage (Addicott, 1976) of Washington and Oregon (Masuda and Addicott, 1970; Addicott, 1976, 1977, 1978, 1981). By the end of the Late Miocene, the genus *Masudapecten* had become extinct in the northwest Pacific.

The history of the Recent *M. yessoensis* began in the Early Pliocene (Fig. 6). *M. nakatombetsuensis*, known from the Upper Miocene Nakatombetsu Formation of northeastern Hokkaido is, most probably, its direct ancestor. During the Pliocene, the range of *M. yessoensis* extended as far as western Kamchatka, and it is quite common there in deposits of the Enemtsenskaya suite (Sinelnikova, 1975; Sinelnikova *et al.*, 1979), and in Honshu and Hokkaido. In Japan, this species is characteristic of the Early Pliocene Omma-Manganzian fauna, but there are no reliable records of *M. yessoensis* from Pliocene deposits of Sakhalin and the Kurile Islands. In eastern Honshu it was partially substituted by the subspecies *M. yessoensis pseudoyessoensis*. *M. yokoyamae* was also a related species. During the Late Pliocene, the range of *M. yessoensis* decreased sharply and became very similar to its Recent range.

During the Early Pliocene *Fortipecten* species were widely distributed in Japan, Sakhalin and Kamchatka (see: Noda *et al.*, 1982, fig. 3). At this time, *Fortipecten* species spread also as far as the North Pacific coast of America (Masuda, 1971; Addicott, 1974), where the genus is represented by *F. hallae* in deposits of the Beringian and Anvilian transgressions in Alaska, and in the Ustj-Limimtevyamakaya suite of Karaginsky Island (Sinelnikova, 1975).

During the Early Pliocene, the originally continuous range of *Mizuhopecten* in the North Pacific appears to have become disjunct (Fig. 7). The relic range of the genus, represented by *M. warreni* descendants, per-

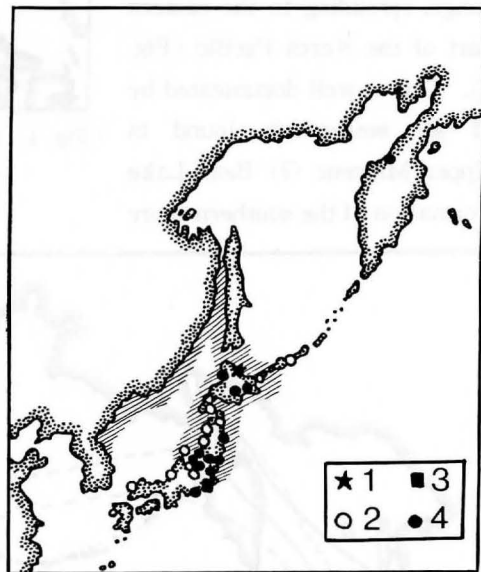


Fig. 6. Geographical and geological distribution of *Mizuhopecten yessoensis* and related forms during the Neogene. 1; *M. nakatombetsuensis* (Late Miocene), 2; *M. yokoyamae* (Early Pliocene), 3; *M. yessoensis pseudoyessoensis* (Early Pliocene), 4; *M. yessoensis yessoensis* (Early and Late Pliocene). The Recent range of *M. yessoensis* is shaded.

sisted for some time in Washington and adjacent areas. During the late Pliocene, the majority of *Mizuhopecten* species and all *Fortipecten* species became extinct, the species diversity of *Mizuhopecten* decreased sharply (Fig. 1), and its geographic range approached that of the Recent *M. yessoensis*. At the end of the Pliocene and during Early Pleistocene time, the subfamily is represented, in addition to the common Japanese scallop *M. yessoensis*, only by *M. tokyoensis*, including a geochronological cline: *M. tokyoensis hokurikuensis* from the Lower Pliocene of southern Kyushu and southeastern Honshu, *M. tokyoensis tokyoensis* from the Upper Pliocene and Lower Pleistocene of southern Kyushu, eastern Honshu and Hokkaido, and *M. tokyoensis semataensis* from the Middle Pleistocene of central Honshu. Only *M. yessoensis* has persisted from the Early Pliocene to the present.

In comparison to *Mizuhopecten*, *Patinopecten* is a much younger group. The history of its establishment and evolution has been reconstructed as follows (Addicott, 1972, 1974, 1976, 1977, 1981; Allison, 1978; Masuda, 1978). The first member of the genus belong to the subgenus *Patinopecten (Lituyapecten)* and appeared during the Early Miocene in Alaska (Fig. 8), with the southern limit of their range not extending beyond 53–58° N. The ancestors of *Patinopecten (Lituyapecten)* were species of *Vertipecten* Grant and Gale, 1931, which has occurred along the Pacific coast of North America since Eocene time. This opinion is shared by several authors (MacNeil, 1961; Masuda, 1962; Moore, 1963; Addicott, 1974), irrespective of their concepts of the taxonomic relationships of Asian and American "*Patinopecten*", i.e., *Mizuhopecten* + *Patinopecten* s.s.

During the Early Miocene, *Vertipecten* species were widely distributed along most of the Pacific coast of North America, from California to northern Alaska, with *V. fucanus* (Dall, 1898) being a zonal species of the Pillarian Stage (Addicott, 1976) in British Columbia, Washington and Oregon. *Patinopecten (Lituyapecten)* is likely to have separated from *Vertipecten* in the northern part of its range. At the end of the Early Miocene and the beginning of the Middle Miocene, *Patinopecten (Lituyapecten)* gave rise to true *Patinopecten*, the only living re-

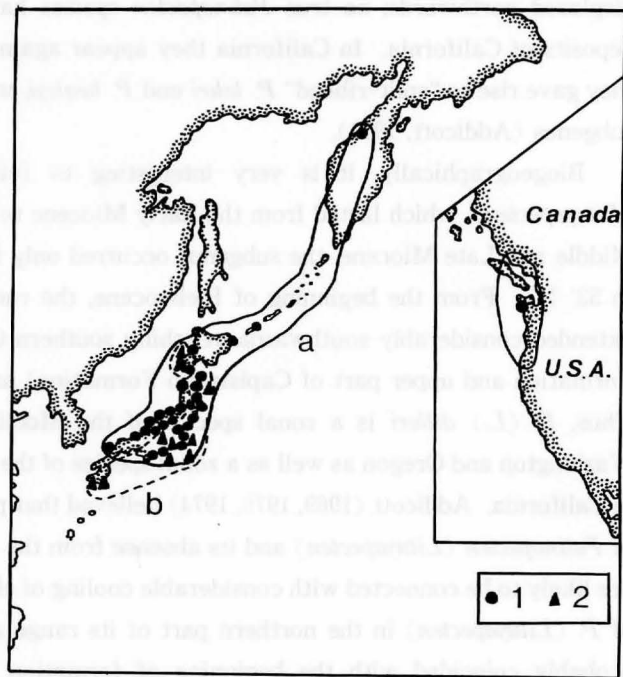


Fig. 7. Geographical and geological distribution of *Mizuhopecten* species during the Early (1) and Late (2) Pliocene. The range limits: a; Early Pliocene, b; Late Pliocene.

prestate of which, *P. caurinus* (Gould, 1850), has survived from the Pliocene to the present) similar to *M. yessoensis* among Fortipectininae).

During the Middle Miocene, *Patinopecten* s.s. occurred from British Columbia to California (Fig. 8). It appeared almost at the same time in the northern and in the southern parts of its range: in the Newportian Stage of the Pacific North-West of the U. S. A. and in the Temblor Stage of California. In particular, *P. propatulus* (Conrad, 1849) is a zonal species for the Newportian Stage.

During the Late Miocene, the southern limit of *Patinopecten* s.s. appears to have been displaced northwards; no true *Patinopecten* species have been found in Upper Miocene deposits of California. In California they appear again only in the Early Pliocene, where they gave rise to "split-ribbed" *P. lohri* and *P. healeyi*, which can be regarded as a separate subgenus (Addicott, 1974).

Biogeographically, it is very interesting to follow the history of *Patinopecten* (*Lituyapecten*), which lasted from the Early Miocene to the Early Pleistocene. During the Middle and Late Miocene, the subgenus occurred only in the Gulf of Alaska (southwards to 53° N). From the beginning of Pleistocene, the range of *Patinopecten* (*Lituyapecten*) extended considerably southwards, reaching southern California (lower part of Fernado Formation and upper part of Capistrano Formation) and even Baja California (27.5° N). Thus, *P. (L.) dilleri* is a zonal species of the Moclipsian Stage in British Columbia, Washington and Oregon as well as a zonal species of the Etchegoin and San-Joaquin stages in California. Addicott (1969, 1970, 1974) believed that post-Miocene southward migration of *Patinopecten* (*Lituyapecten*) and its absence from the Upper Pliocene deposits of Alaska are likely to be connected with considerable cooling of climate at that time. The extinction of *P. (Lituyapecten)* in the northern part of its range and its southward migration most probably coincided with the beginning of formation of amph-Pacific disjunctions of marine biota, which took place during the late Miocene and early Pliocene (Kafanov, 1974, 1982).

Thus, an analysis of the phylogenetic and geochronological relationships of the two

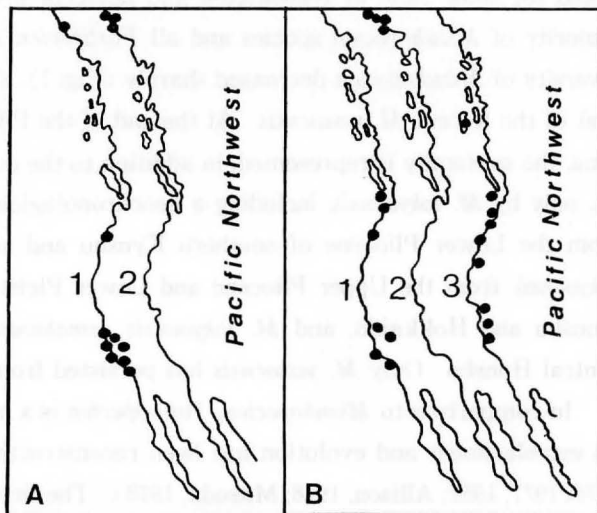


Fig. 8. Geographical and stratigraphical distribution of *Vertipecten* (1), *Patinopecten* (*Lituyapecten*) (2) and *Patinopecten* s.s. (3) species during the Early (A) and Middle (B) Miocene (from: Addicott, 1974, text-figs. 3-4; adapted and modified.)

subfamilies of Pectinidae (Fig. 3) has allowed us to arrive at the following conclusions. Fortipectininae is a typical group of near-Asian Pacific origin, which developed in the northern Japan-Sakhalin Paleogene province in the Late Oligocene. Some members of Fortipectininae—species of the genera *Mizuhopecten* and *Fortipecten*—migrated to the American coast of the North Pacific during the Late Miocene and Early Pliocene. The Patinopectininae is a group of Neogene genesis, and the development and further evolution of this group is wholly connected with the Pacific coast of North America. *Patinopecten* has never spread to the North-West Pacific. This is an additional and quite important argument for regarding *Mizuhopecten* (Fortipectininae) and *Patinopecten* (Patinopectininae) as two separate genera with independent phylogenetic development.

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