958. EARLY EVOLUTION AND DISTRIBUTION OF THE GASTROPOD GENUS NUCELLA, WITH SPECIAL REFERENCE TO MIocene SPECIES FROM JAPAN*

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Abstract. Several well preserved specimens of the muricid gastropod genus Nucella from Miocene strata in Hokkaido, Japan, are classified into two species, N. tokudai (Yokoyama) and N. freycineti saitoi Hatai et Kotake. N. tokudai first appeared in California during the Early Miocene, and then spread westward to Japan and Kamchatka by the early Middle Miocene. N. freycineti saitoi first appeared in Japan during the Middle Miocene, and gave rise to a living species, N. f. freycineti (Deshayes) during the latest Miocene or Early Pliocene. A warm-water origin in the northeastern Pacific is postulated for the genus Nucella, based on the early geographical distribution of the genus and on the presence of a thick denticulated outer lip in all early species. The distributional history of Nucella, characterized by a warm-water origin in western North America and subsequent dispersal to eastern Asia, is similar to that of many other shallow-water temperate North Pacific molluscs and barnacles.

Key words. Miocene, Nucella, Gastropoda, evolution, biogeography.

Introduction

The modern muricid gastropod genus Nucella is commonly known and widely distributed on the shore of the North Pacific and North Atlantic Oceans. Its members are predators of barnacles (Cirripedia), mussels (Mytilidae), and limpets (Acmaeidae). In northern Japan, most authors recognize two Recent species, N. freycineti (Deshayes) and N. heyseana (Dunker) (e.g. Habe and Ito, 1965). Mitochondrial DNA sequences show that there are two species among the genus Nucella in northern Japan (Collins et al., in preparation). The small N. freycineti is living in the middle and upper intertidal zone, and the larger N. heyseana (Dunker) is in the lower intertidal and shallow sublittoral zones.

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(Collins et al., in preparation). It is possible that *N. elongata* Golikov et Kussakin is synonymous with *N. heyseana*, but the limits of the species of *Nucella* in the northwestern Pacific are not well understood.

Little is known about the early evolution and geographical distribution of *Nucella*. The genus first appeared in the Early Miocene of western North America (Loel and Corey, 1932). Some time later, *Nucella* reached the northwestern Pacific, but the scarcity of adequate fossil material has made it difficult to treat the history of the genus *Nucella* in Asia in detail. The earliest appearance of *Nucella* in the Atlantic was in the Late Pliocene of the North Sea Basin in Europe (Vermeij, 1991a, 1993; Collins et al., in preparation). *Nucella* is therefore one of a large number of cold-water animal and plant genera that invaded the North Atlantic from the North Pacific after Bering Strait opened during middle Pliocene time (Durham and MacNeil, 1967; Vermeij, 1991a).

Previous authors have figured only three specimens of *Nucella* from Miocene strata in Hokkaido. Yokoyama (1932) described *Coralliophila tokudai* from the Okada Beds (=early Middle Miocene Horoshin Formation?) in the Uryu coal-field, Northwest Hokkaido. Mizuno et al. (1969) illustrated *Nucella ishii* Uozumi (MS) from the Kushiro coal-field in eastern Hokkaido. Finally, Amano (1983) treated one poorly preserved specimen of *Nucella* from the Late Miocene Upper Togeshita fauna, but he was unable to assign the shell at the species level. These three specimens were not compared with each other, nor were they compared with fossil or living species found elsewhere in the North Pacific region.

We have had an opportunity to examine the holotype of *Coralliophila tokudai* and to collect additional well preserved materials belonging to *Nucella* from several Miocene formations in Hokkaido. Our purpose of this paper is to describe this Miocene material and to discuss the early evolution and geo-

**Localities of the Miocene *Nucella* in Hokkaido**

Two species of *Nucella* were distinguished among specimens from seven localities of Miocene age in Hokkaido (Figure 1). These localities, together with stratigraphical and facies details, are described briefly below.

**Loc. R-1.** Small riverside cliff near Kasugacho-danchi, Rumoi, northwest Hokkaido; medium-grained sandstone; upper part of the Togeshita Formation.

**Loc. R-2.** Bank of Rumoi River near Owada (Rumoi-shinkawa, Loc. T24 of Amano, 1983); pebble-bearing muddy fine-grained sandstone; upper part of the Togeshita Formation.

**Loc. C-1.** Riverside cliff at about 1.1 km upstream of Tanzan-zawa, a small tributary of Chepotsunai River, Tomamae-cho, northwest Hokkaido; pebble-bearing fine-grained sandstone; Chikubetsu Formation.

**Loc. U-1.** Bank of Tokushibetsu River near Kotobuki Bridge, Utanobori-cho, northeast Hokkaido; muddy fine-grained sandstone; Tachikaraushinai Formation.

**Loc. A-1.** Roadside cliff at about 5.2 km upstream of Sarusarube River, Urahoro-cho, eastern Hokkaido; muddy fine-grained sandstone; Ishizawa Formation.

**Loc. A-2.** River bank at about 1.6 km upstream of Ishii-zawa; pebble-bearing muddy fine-grained sandstone; Ishizawa Formation.

**Loc. A-3.** Streamside cliff at about 1.2 km upstream of Tanzan-no-sawa; pebble-bearing medium-grained sandstone; Ishizawa Formation.
Figure 1. Localities of Miocene Nucella in Hokkaido (using the topographical maps of "Rumoi", "Sankai", "Ochube", "Atsumai" and "Ombetsu", scale 1: 50,000 published by Geographical Survey Institute of Japan).
Systematic description

Family Muricidae Rafinesque, 1815
Subfamily Ocenebrinae Cossmann, 1903
Genus Nucella Röding, 1798

Nucella tokudai (Yokoyama, 1932)

Figure 2-2a-b, 4a-b, 5, 7a-b, 8

Coralliophila tokudai Yokoyama, 1932, p. 235-236, pl. 2, fig. 1.
Thais (Stramonita) carrizoensis Loel and Corey, 1932, p. 249-250, pl. 47, figs. 2, 3a-b.
Nucella packi (Clark) var. talea Stewart, 1946, p. 102, pl. 17, fig. 11.
Thais sp., Lutz, 1951, p. 392, pl. 18, figs. 2, 5.
Thais lima (Gmelin), Hall, 1958, pl. 9, figs. 7, 10.
Thais packi Clark. Addiccott, 1965, fig. 3R.
Nucella ishii Uozumi (MS). Mizuno et al., 1969, pl. 28, fig. 2.
Thais (Nucella) packi Clark. Addiccott, 1970, p. 84-85, pl. 9, figs. 1-4, 19.
Nucella packi (Clark). Addiccott, 1980, pl. 1, fig. 6; Gladenkov and Sinelnikova, 1990, p. 126-127, pl. 19, figs. 4, 16.

Type locality.—Gengoro-sawa, Numata-cho, Hokkaido. CM no. 26003 (Figure 2-8).

Materials.—Two specimens from the Togeshita Formation (Loc. R-1), one specimen from the Chikubetsu Formation (Loc. C-1), and seven specimens from the Ishizawa Formation (Loc. A-1, 2, 3).

Description.—Shell small to medium, heavy, bucciniform, with very low spire. Whorls more than four. Suture poorly defined. Surface ornamented with flat-topped spiral ribs and weak growth lines. Spiral ribs 15 to 19 on body whorl, 4 to 8 on penultimate. Aperture large, ovate. Siphonal canal very short and deep. Outer lip thick with 13 to 16 teeth.

Measurements (in mm).—

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*number of spiral cords on body whorl.

Remarks.—The present species was originally described by Yokoyama (1932, August) from the Middle Okada Beds in Hokkaido under the genus name Coralliophila. The species has subsequently been mentioned by Hatai and Nisiyama (1952), Uozumi (1962), Ohara (1966) and Ohara and Kanno (1973). N. tokudai is characterized by very low spire, thick outer lip with numerous small teeth and numerous flat-topped spiral ribs of even strength, which are separated by rather deep grooves.

Loel and Corey (1932, December) proposed Thais (Stramonita) carrizoensis from the Early Miocene Vaqueros Formation in California. The holotype of this species has 11 flat-topped spiral ribs on the body whorl. Although this number of ribs is smaller than the typical N. tokudai, all other characters of T. carrizoensis conform with those of N. tokudai. Moreover, according to Addiccott (1970) and our own observations, other specimens of T. carrizoensis have more numerous ribs. We therefore regard Loel and Corey’s species as a junior subjective synonym of N. tokudai.

Addiccott (1970) considered Thais carrizoensis to be a junior subjective synonym of

→ Figure 2. 1a-b, 3, 11a-b, 12: Nucella freycineti saitoi Hatai et Kotaka. 1a-b: ×1, Loc. R-1, Togeshita Formation, IGUT no. 11801. 3; ×2, Loc. U-1, Tachikaraushina Formation, JUE no. 15402. 11a-b: ×1, Loc. R-2, Togeshita Formation, JUE no. 15403. 12; ×1, Loc. R-2, Togeshita Formation, IGUT no. 11803. 2a-b, 4a-b, 5a-b, 7a-b, 8: Nucella tokudai (Yokoyama). 2a-b; ×2, Loc. C-1, Chikubetsu Formation, JUE no. 15404. 4a-b, 5a-b; ×1, Loc. A-1, Ishizawa Formation, JUE no. 15405. 7a-b; ×1, Loc. R-1, Togeshita Formation, IGUT no. 11802. 8; ×2, holotype (CM no. 26003). 6, 9: “Nucella” tokshiensis Itoigawa et Shibata. 6; ×1.5, paratype (MFM no. 10078). 9; ×1.5, holotype (MFM no. 10076). 10: Nucella freycineti (Deshayes), ×1, Loc. Rumi, Recent, JUE no. 15406.
Thais packi, which was described by Clark (1918) from the Late Oligocene or earliest Miocene San Ramon Formation in California. T. packi, which was assigned to Nucella by Stewart (1946), is very similar to T. carrizoensis in shell outline and sculpture. The holotype of T. packi, however, possesses a small labral tooth near the base of the outer lip. This feature is also preserved on several other specimens from the San Ramon Formation. The presence of this labral projection indicates that T. packi belongs to either Acanthina or Acanthinucella. Because of the position of the spine and the nature of the shell sculpture, we tentatively assign the species to the genus Acanthinucella (for a discussion of distinctions among Nucella, Acanthina, Acanthinucella, see Vermeij, 1993). Specimens assigned to T. packi from other Miocene strata in western North America and Kamchatka by Addicott (1965, 1970, 1980) and Gladenkov and Sinelnikova (1990) lack the labral projection. They can therefore be assigned to N. tokudai.

Polytropa ishii was listed by Uozumi (1962) as a representative species of the Miocene Atsunai-Togeshita fauna, but Uozumi neither illustrated nor described the material upon which this name was based. In their survey of the fauna of the Atsunai area in eastern Hokkaido, Mizuno et al. (1969) figured one specimen from the “Atsunai Formation” (= Ishizawa Formation) as Nucella ishii Uozumi (MS). In our examination of specimens from this formation, we were unable to detect differences between N. ishii and N. tokudai. Therefore, we regard N. ishii as a junior subjective synonym of N. tokudai.

Comparison.—The present species is similar to the northeastern Pacific Recent species Nucella canaliculata (Duclos), especially, to the form described by Dall (1915) as the variety compressa. The latter form has a low spire and numerous flat-topped spiral ribs with narrow interspaces. However, N. canaliculata differs from N. tokudai by having fewer spiral cords on the body whorl (12 to 13 in N. canaliculata as compared to 15 to 19 in N. tokudai), and by having generally thin outer lip without denticles on the inner surface.

Several species of “Nucella” or “Polytropa”

![Figure 3. Distribution of Nucella tokudai (Yokoyama).](image-url)
have been recorded from early Middle Miocene deposits in Honshu, but none belongs to Nucella. Among them, "Nucella" tokishiensis (Figure 2–6, 9) was described from the Nataki Conglomerate and the Shukunohora Sandstone in Gifu Prefecture by Itoigawa and Shibata (1976). This species resembles N. tokudai in having 16 to 17 flat-topped spiral cords on the body whorl, but it differs by being more slender, by the presence of 9 to 12 low axial ribs on the penultimate whorl, especially by the presence of a knob at the posterior end of the inner lip (see also Horikoshi, 1983). The inner-lip knob is absent in nearly all species of Nucella; it is present only in the Californian N. emarginata (Deshayes), a highly derived member of the genus (Vermeij, 1993; Collins et al., in preparation).

Distribution.—Early Miocene Vaqueros Formation and Jewett Sand, California; early Middle Miocene Chikubetsu and Middle Okada Beds, Hokkaido, and Kakert Suite, western Kamchatka; Middle Miocene Tembor Formation, Sobrante Sandstone, California, and Astoria Formation and Sandstone of Floras Lake, Oregon, and Ishiizawa Formation, Hokkaido; Late Miocene upper part of the Togeshita Formation, Hokkaido, and Cierbo Sandstone, California (Figure 3).

Nucella freycinetii saitoi Hatai and Kotaka, 1959

Figure 2–1a–b, 3, 11a–b, 12.


Nucella sp., Amano, 1983, p. 33, pl. 8, fig. 25.

Thais lima (Martyn). Gladenkov et al., 1984, p. 245, pl. 62, figs. 4a–b

Type locality.—Okamami-zawa, Obanazawa-machi, Yamagata Prefecture. IGPS no. 77797.

Materials.—Four specimens from the Togeshita Formation (Loc. R-1, 2) and one specimen from the Tachikaraushinai Formation (Loc. U-1)

Description.—Shell large for the genus, solid, bucciniform, with low spire. Whorls more than four. Surface ornamented with round-topped spiral cords, weak growth lines; low secondary spiral riblets in broad interspaces between cords; 18 to 20 cords and riblets on body whorl, 3 to 8 on penultimate whorl. Aperture large, ovate. Siphonal canal narrow and short. Fasciole rather prominent. Inner lip smooth, covered with thin callus. Outer lip thick, with 8 denticles on its inner surface. These denticles distinct on young specimens, obsolete on adults.

Measurements (in mm).—

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*number of spiral cords and riblets on body whorl.

Remarks and comparison.—The present subspecies was proposed by Hatai and Kotaka (1959) for material from the Middle Miocene Ginzan Formation in Yamagata Prefecture, Northeast Honshu. In their paper, they misspelled the specific name, as freycinetii. N. f. saitoi is distinguished from the Recent N. f. freycinetii (Figure 2–10) and N. heysana by the thicker outer lip, narrower aperture, and by the presence of 8 denticles on the inner side of the outer lip. As pointed out by Hatai and Kotaka (1959), the shell length : breadth ratio of Recent adult specimens is greater than that of the fossil N. f. saitoi. The fossil species lacks the axial sculpture often observed in N. heysana. In other respects, however, N. f. saitoi is very similar to the Recent N. f. freycinetii.

Amano (1983) described and illustrated one poorly preserved specimen of Nucella from the Late Miocene upper part of the Togeshita Formation in Rumoi, northwest Hokkaido, but did not assign the shell at the
species level. Several well preserved specimens have been collected since from the same site (Loc. R-2=T24 of Amano, 1983). These conform in characters of sculpture and outer lip to *N. f. saitoi*.

Gladenkov *et al.* (1984) recorded *Thais lima* (Martyn) from the Middle Miocene Etolon Suite in western Kamchatka. Judging from their description and illustration, we believe the material from Kamchatka should be referred to *Nucella freycineti saitoi*. Gladenkov *et al.* (1984) described it as having 14 to 15 round-topped spiral cords with some interstitial riblets, and possessing a thick outer lip with some crenulations. The figured specimen has a lower spire than does the type of *N. f. saitoi*, but, as spire height tends to be a highly variable character within

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**Figure 4.** Distribution of *Nucella freycineti saitoi* Hatai et Kotaka.
species of *Nucella*, it is therefore unreliable for distinguishing among species. Typical *Nucella lima* (Gmelin) has a thin outer lip without denticles.

**Distribution.**—Middle Miocene Ginzan and Tachikaraushinai Formations, northern Japan, and Etolon Suite, western Kamchatka; Late Miocene upper part of the Togeshita Formation, Hokkaido (Figure 4).

**Early evolution and migration of *Nucella* in Miocene**

The evolutionary origins of *Nucella* remain obscure, but the available evidence indicates that the genus arose in the warm-temperate northeastern Pacific. The earliest record of *Nucella* is of *N. tokudai* from the Vaqueros Formation and Jewett Sand (Early Miocene) in California (Loel and Corey, 1932; Addicott, 1965, 1970). *N. tokudai* is extremely similar to Clark’s (1918) *Thais packi* from the San Ramon Formation (Late Oligocene or earliest Miocene) in California. *Thais packi*, which we here tentatively assign to *Acanthinucella*, differs from *N. tokudai* only by the presence of a small labral projection. In view of this similarity, it is likely that the two species share a common ancestry.

The earliest northwestern Pacific records of *Nucella* are those of *N. tokudai* from the early Middle Miocene in Hokkaido and Kamchatka. These records indicate that *N. tokudai* spread westward from California to Japan by the early Middle Miocene, which corresponds to the time of the so-called climatic optimum of the Miocene. Hokkaido at this time lay in a mild- to cool-temperate zone (Ogasawara, 1988). Many warm-water species extended quite far north in the Pacific at that time (Marincovich, 1984). Exactly when and how the dispersal of *N. tokudai* occurred is not known. Miocene records of *Nucella* are lacking in Alaska, possibly because the warm-water populations of early *Nucella* were not adapted to the cold conditions postulated to have existed in parts of Alaska during the early Middle Miocene by Marincovich (1990).

Several other shallow-water gastropod genera had invasion histories similar to that of *Nucella*. These include *Littorina* (Reid, 1989, 1990) and the buccinid *Lirabuccinum* (Vermeij, 1991b). These genera had earlier records in western North America than in eastern Asia, and evidently crossed the North Pacific westward by early Middle Miocene time. The same may be true for several genera of barnacles, including *Chirona* and *Hesperibalanus* (Zullo and Marincovich, 1990). Large rugose mussels of the genera *Plicatomytilus* and *Tumidimytilus* also achieved a broad amphipacific distribution during the early Middle Miocene (Allison and Addicott, 1976; Kafanov, 1987; Uozumi and Akamatsu, 1988). Thus, by the Middle Miocene, many of the shallow-water organisms with which *Nucella* lives and upon which it feeds were widespread throughout the North Pacific.

The second species of *Nucella* to appear in the northwestern Pacific was *N. freycineti saitoi*, which is known from the Middle Miocene Tachikaraushinai and Ginzan Formations in Japan and the Etolon Suite in Kamchatka. Shibata et al. (1981) assigned an age of 13.7–13.8 Ma to the Tachikaraushinai Formation by K/Ar dating method.

*N. f. saitoi* persisted into the Late Miocene upper part of the Togeshita Formation, which contains some molluscs in common with those from the Pliocene Sannohe Group in Northeast Honshu and the Plio-Pleistocene Omma-Manganji fauna in the Japan Sea Borderland (Amano, 1986). The oldest *N.f. freycineti* was described by Chinzei (1961) from the Togawa Formation of the Sannohe Group. It is likely that this form evolved from *N. f. saitoi* during latest Miocene or Early Pliocene time.

The Miocene species of *Nucella* from Japan differ from their living counterparts in the northwestern Pacific by having an exceptionally thick outer lip whose inner side is
denticulate. An outer lip of this kind is commonly seen in tropical gastropods and is suspected to have an antipredatory function (Vermeij, 1987). It is likely that *Nucella* arose and spread in relatively warm waters, where predators are abundant. Subsequently, several lineages of *Nucella* became adapted to cooler waters, where the outer lip became thinner and the denticulation was lost, as in *N. f. freycineti*, *N. heyseana*, *N. lima*, and most populations of *N. canaliculata*. However, other lineages of *Nucella* retained or reacquired thick denticulate lips. This applies to the northeastern Pacific *N. lamellosa* (Gmelin) and the north Atlantic *N. lapillus* (Linnaeus). The Californian *N. emarginata* has secondarily adapted to warmer waters and, at least in populations from sheltered sites, has evolved a very thick, strongly denticulate lip (Collins et al., in preparation).

The early evolution of *Nucella* illustrates the important point that many shallow-water elements of the present-day temperate North Pacific fauna arose in relatively warm waters and soon thereafter spread throughout the North Pacific Basin. Because most previous studies of the fossil faunas of this region have been restricted to particular areas, comparisons of specimens from different parts of the North Pacific have often not been made. As a result, the number of groups like *Nucella* whose geographical distributions came to encompass large parts of both the eastern and western North Pacific is probably much larger than the available literature now indicates. Many more examples will doubtless come to light when detailed comparisons are made between faunas of western North America and eastern Asia.

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958. Early evolution of *Nucella*


Kazutaka Amano, Geerat J. Vermeij and Ken Narita


Kasuga-cho 富町, Rumoi 留萌, Togeshita 塚下, Owada 大和田, Tanzan-zawa 炭山沢, Tomamae 萩前, Utanobori 歌並, Urahoro 浦幌, Ishii-zawa 石井沢, Tanzan-no-sawa 炭山の沢。

*Nucella* 属 (腹足類) の初期進化と分布。特に日本産中新世種について: 北海道の中新統から産出したアキガイ科の腹足類, *Nucella* の保存の良い標本は *N. tokudai* (Yokoyama) と *N. freycinetii saitoi* Hatai et Kotaka に同定される。*N. tokudai* は中新世前期にカリフォルニアに出現し, 中期中新世初期までに, 西方へ日本およびカムチャッカに分布を広げた。*N. freycinetii saitoi* は中新世中期に日本に出現し, 本亜種から中新世末期または鮮新世前期に現生の *N. freycinetii* (Deshayes) が進化した。初期の地理的分布や初期のすべての種に小歯をともなう厚い外殻が見られることから, *Nucella* 属は北東太平洋の温暖水起源であることが推定される。北米西岸の温暖水起源をもと, その後東アジアに分散した *Nucella* の分布の変遷は, 北太平洋の温帯浅海域の他の多くの貝類やフジノポの分布の変遷史に類似している。