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The identity of the large "*Mytilus*" (Mollusca: Bivalvia: Mytilidae) from the lower Miocene Iwamura Group, central Japan

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Abstract

The large mytilid, previously identified as the modern species *Mytilus coruscus* Gould, 1861, from the lower Miocene Iwamura Group of central Japan, is reexamined taxonomically on the basis of newly obtained well-preserved specimens. Careful observation of these specimens reveals that they can be reidentified as another modern species, *Crenomytilus grayanus* (Dunker, 1853). This unequivocally is the oldest record of *C. grayanus*, extending its stratigraphic range back to the upper lower Miocene. The fossil record of *M. coruscus* in the Japanese Neogene requires a taxonomic re-evaluation.

Keywords: Mytilidae, *Mytilus coruscus*, *Crenomytilus grayanus*, Miocene, Iwamura Group, Gifu Prefecture

Introduction

The genus *Mytilus* is one of the most cosmopolitan of all marine genera, occurring at higher latitudes in all oceans and major seas of both Northern and Southern Hemispheres (Seed, 1992). Carter and Seed (1998) briefly reviewed the fossil record of *Mytilus* and its related genera, and stated that the known Cenozoic fossil record of *Mytilus* does not begin until the Oligocene. Vermeij (1991) suggested that *Mytilus* invaded the North Atlantic from the North Pacific after the early Pliocene opening of the Bering Strait between Alaska and Siberia. On the basis of phylogenetic data, Hilbish *et al*. (2000) revealed that *Mytilus* in the Southern Hemisphere arose from a migration event from the Northern Hemisphere during the Pleistocene via an Atlantic route. Therefore, documentation of the taxonomy and biogeographic history of *Mytilus* in the Japanese Miocene is crucial for understanding the early evolution of the genus.

Fossils of large mussels occasionally occur in the Miocene shallow marine deposits in Japan. Among them, the Miocene extinct subgenera *Mytilus* (*Tumidimytilus*) and *M.* (*Plicatomytilus*) attracted paleontologist's attention because of their biostratigraphic utility and peculiar shell morphology (*e.g.*, Uozumi, 1966; Uozumi and Akamatsu, 1988; Noda and Hoyanagi, 1993; Yoshida, 1998; Kurihara *et al*., 2005). On the other hand, fossils of the extant clades *Mytilus* (s.s.) and *Crenomytilus* have been listed and sometimes illustrated from the Japanese Miocene, but their shell morphology was rarely discussed in detail. Therefore, the taxonomy and biogeographic history of these clades remain uncertain.

A large species of fossil mytilid bivalve from the lower Miocene Iwamura and Mizunami Groups in central Japan has previously been referred to the modern species *Mytilus coruscus* Gould, 1861 (*e.g.*, Itoigawa, 1960; Itoigawa *et al*., 1974, 1981, 1982; Shibata, 1978; Ujihara *et al*., 1992; Okumura and Karasawa, 1994). On the basis of careful examination of additional specimens from the Iwamura Group, it became clear that it is not referable to *M. coruscus* but to another modern species, *Crenomytilus grayanus* (Dunker, 1853). We describe here *C. grayanus* from the Iwamura Group and demonstrate the taxonomic distinction between *C. grayanus* and *M. coruscus*.

The measurement protocol and morphological terms used in this study follow Seed (1992) and Carter *et al*. (2012). The specimens illustrated in this study are deposited in the Mizunami Fossil Museum (MFM). Details of the locality information are given in the Appendix. In the figure captions, shell length, height and width are abbreviated as L, H and W, respectively.

Geologic settings

The Iwamura and Mizunami Groups are representative

strata of the "eastern Setouchi Miocene Series" distributed in Gifu Prefecture, central Japan, and their stratigraphy and correlation were summarized in Irizuki *et al*. (2004). The Iwamura Group is composed of the lower Agi Formation (non-marine and brackish deposits) and the upper Toyama Formation (marine deposits). The Kubohara facies is the basal/marginal unit of the Toyama Formation and unconformably overlaps the basement rocks. It is a 5 to 15 m-thick, fossiliferous unit that consists of conglomerate or gravelly sandstone and siltstone. The Toyama Formation contains diatom fossils of the upper lower Miocene and is correlated to the Akeyo Formation of the Mizunami Group by key beds and diatom fossils (Irizuki *et al*., 2004). Molluscan assemblages from the Iwamura Group were described by Itoigawa (1955) and Shibata (1978). Shibata (1978) and Ujihara *et al*. (1992) recognized *Mytilus coruscus* in the Kubohara facies, without providing an illustration. Irizuki *et al*. (2004) analyzed ostracode fossils from the Iwamura Group and discussed their paleoenvironment. The mytilid specimens examined here were recovered from a 30 cm-thick shell bed of the uppermost Kubohara facies of the Toyama Formation in an outcrop at Shimogahora in the Iwamura Basin (see Appendix). This locality is the same one from where Okumura and Karasawa (1994) illustrated mussel pearls and shells under the name *Mytilus coruscus*. The associated molluscs are characterized by a mixture of soft- and hard-bottom dwellers and include the following genera such as *Acila*, *Nuculana*, *Saccella*, *Arca*, *Porterius*, *Septifer*, *Lithophaga*, *Chlamys*, *Monia*, *Lucinoma*, *Cyclocardia*, *Clinocardium*, *Saxidomus*, *Phacosoma*, *Nipponomarcia*, *Ruditapes*, *Humilaria*?, *Anisocorbula*, *Diodora*, *Protorotella*, *Homalopoma*, *Liotina*, *Lunella*, *Nerita*, *Turritella*, *Cerithium*, *Calyptraea*, *Crepidula*, *Euspira*, *Cryptonatica* and *Boreotrophon*. The sampling horizon is estimated as ca. 18 Ma in age, and its paleoenvironment was possibly in the central bay near a rocky shore under the influence of temperate water-masses (Irizuki *et al*., 2004).

Systematic paleontology

Family Mytilidae Rafinesque, 1815

Genus *Crenomytilus* Soot-Ryen, 1955

Type species: *Mytilus grayanus* Dunker, 1853, by original designation, Miocene to Recent, northern Japan, Korean Peninsula to Russian Far East.

Emended diagnosis: Shell large, thick, mytiliform, inflated; beaks terminal, protruded; dorsal margin gently expanded; ventral margin gently concave. Sculpture of irregular commarginal lines and periodic step-like undulations; radial striae distinct, especially on the ventral surface. Inner margins, especially the antero-ventral one, finely crenulated. Hinge area extremely thick; interior subumbonal shelf broad, almost smooth, with some marginal teeth present in immature specimens, but obsolete in mature specimens; pseudonymph compact, non-vacuolated; lateral part of ligamental groove broad, with fine growth lines; anterior adductor strong, showing a distinct thickened scar; anterior retractor scar elongate behind umbo; posterior adductor and retractor scars continuous.

Remarks: Superficially similar in shape to the genus *Mytilus* Linnaeus, 1758, the genus *Crenomytilus* Soot-Ryen, 1955 is distinguished by having delicate radial striae on the exterior surface, a finely crenulated inner margin and a non-vacuolated pseudonymph with a broad lateral part of ligamental groove.

The genus *Crenomytilus* is restricted today to the cool-temperate northwestern Pacific, and is represented there by the single species *C. grayanus* (Dunker, 1853), the type species of the genus. Fossils of this genus have been recorded from the Neogene of both the Asian and American side of the middle to high latitude North Pacific. The oldest record is from the upper Oligocene of California (Moore, 1983).

Included species: Besides the type, several nominal species of *Crenomytilus* are known from Oligocene to Pliocene formations in Kamchatka, Alaska, Oregon and California (see Moore, 1983; Marincovich, 1983). Vermeij (1989) suggested that these fossil species may be synonymous with *C. grayanus*.

Some European Cenozoic species were previously assigned to the genus *Crenomytilus* (*e.g*., Harzhauser and Mandic, 2001), but Wesselingh *et al*. (2002) revealed that almost all European Cenozoic mussels, including the species previously assigned to *Crenomytilus*, are not referable to that genus but to the genus *Perna* Retzius, 1788. Moreover, Wesselingh *et al*. (2002) suspected that the large extant northwestern Pacific species *Mytilus coruscus* Gould, 1861 belongs to the genus *Crenomytilus*, but our observations clearly deny this assignment, as mentioned later.

Crenomytilus grayanus (Dunker, 1853)

(Figs. 1, 2E–G, 3B, 4)

Mytilus grayanus Dunker, 1853, p. 84; Yokoyama, 1925a, p. 25, pl. 2, fig. 10; Yokoyama, 1925b, p. 15, pl. 2, fig. 1; Sawada, 1962, p. 66, pl. 2, fig. 22; Ogasawara, 1977, p. 100–101, pl. 7, fig. 10.

Crenomytilus grayanus (Dunker); Soot-Ryen, 1955, pl. 2, figs. 9, 10; Noda *et al*., 1984, p. 3–7, pl. 1, figs. 1–3, pl. 2, figs. 1–3, pl. 3, figs. 1a–2b, pl. 4, figs. 4a, b; Ogasawara *et al*., 1985, p. 32–33, pl. 3, fig. 3; Matsuura, 1985, pl. 40, fig. 26; Ogasawara *et al*., 1986, pl. 31, figs. 3a, b, pl. 45, figs. 1a, b; Akamatsu and Suzuki, 1990, pl. 3, fig. 2; Noda *et al*., 1993, p. 137–138, fig. 15.10; Matsubara, 2009, figs. 7.1, 7.3; Kurihara, 2010, p. 29–30, figs. 12e–g; Ando and Itoigawa, 2018, p. 14–15, pls. 1, 2.

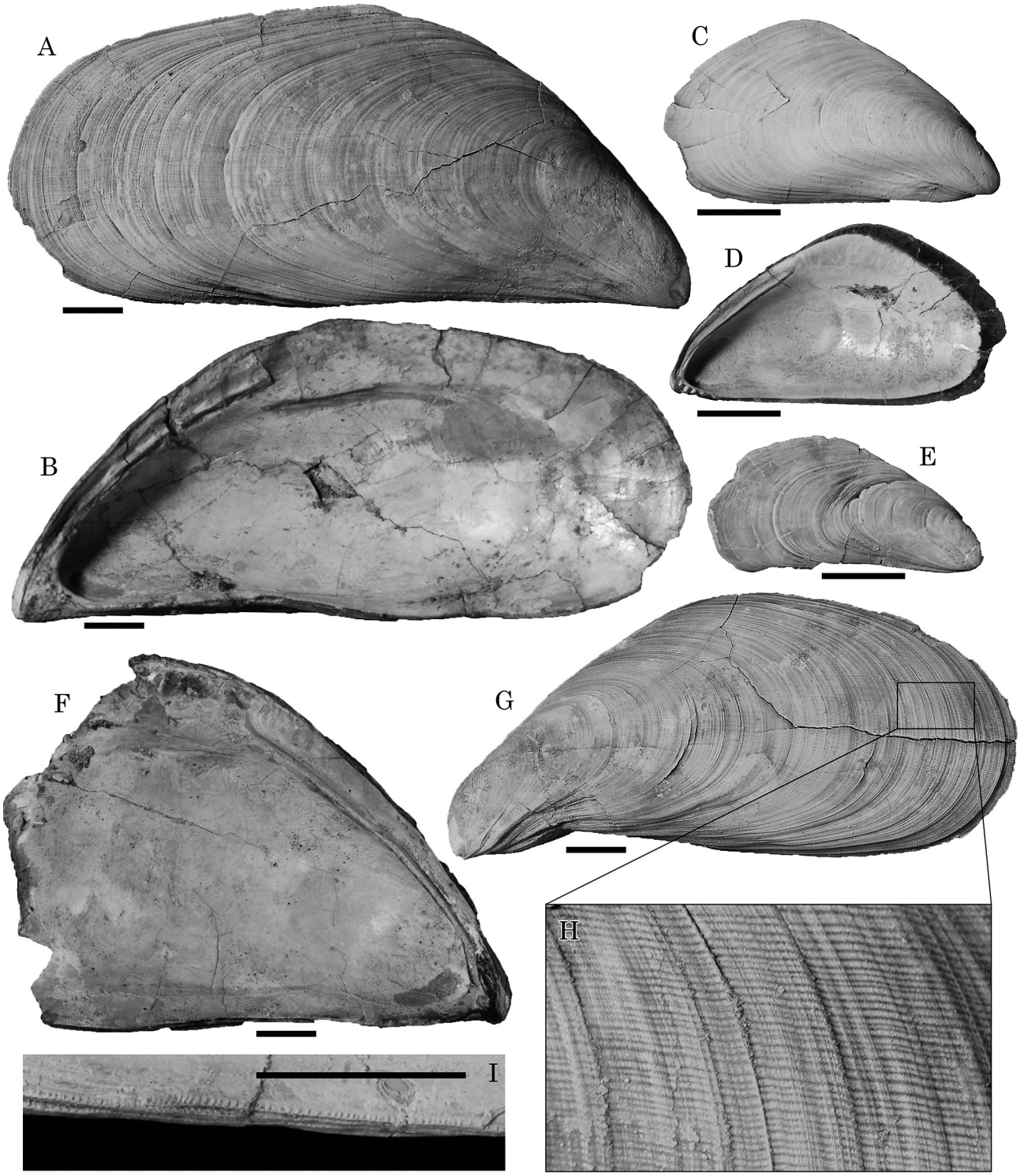


Fig. 1. ***Crenomytilus grayanus*** **(Dunker)** from loc. Shimogahora, from an upper lower Miocene Kubohara facies of the Toyama Formation, Iwamura Group. Exterior coated with ammonium chloride. All scale bars 10.0 mm. **A, B,** exterior and interior of right valve, L: 120.3 mm, H: 53.1 mm, W: 21.1 mm, MFM16015; **C, D,** Exterior and interior of right valve, L: 39.6 mm, H: 21.6 mm, W: 5.9 mm, MFM16016; **E,** Exterior of right valve, L: 33.2 mm, H: 16.3 mm, W: 4.8 mm, MFM16017; **F,** Interior of incomplete left valve, L: 90.6 mm, H: 63.2 mm, W: 22.7 mm, MFM16018; **G, H,** Exterior of left valve and enlargement of central exterior surface showing the delicate fine radial striae, L: 96.8 mm, H: 45.4 mm, W: 20.3 mm, MFM16019; **I,** Enlargement of interior ventral margin of right valve showing the fine crenulations, L: 126.4 mm, H: 60.8 mm, W: 21.1 mm, MFM16020.

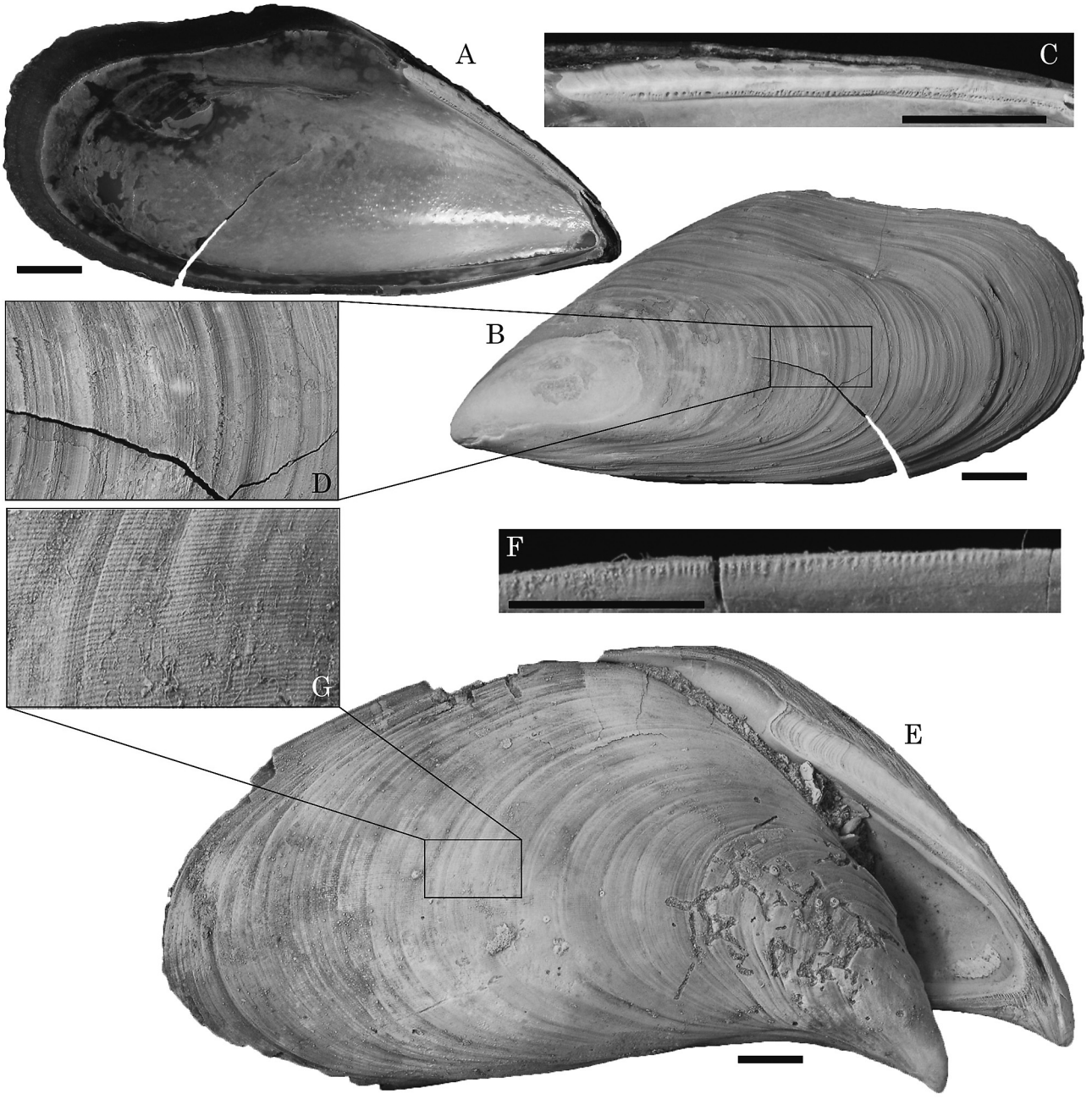


Fig. 2. Comparisons between shells of *Mytilus coruscus* Gould and *Crenomytilus grayanus* (Dunker). Exterior coated with ammonium chloride. All scale bars 10.0 mm, except F (5.0 mm). **A, B, C, D, *M. coruscus*.** Interior, exterior and enlargement of vacuolated pseudonymph and central exterior surface, left valve, L: 102.6 mm, H: 47.3 mm, W: 18.4 mm, MFM150001 from loc. Morai, Recent; **E, F, G, *C. grayanus*.** Right view of slightly displaced specimen, enlargement of dorsal margin of right valve and of central exterior surface of right valve, L: 137.2 mm, H: 68.4 mm, W: 47.9 (conjoined) mm, MFM112461 from loc. Soibetsu, lower Pleistocene Setana Formation.

Mytilus coruscus Gould. Itoigawa, 1960, table 2; Itoigawa in Itoigawa *et al*., 1974, p. 61–62, pl. 7, figs. 6, 7; Shibata, 1978, p. 46; Itoigawa *et al*., 1981, pl. 4, fig. 11; Itoigawa *et al*., 1982, p. 30; Ujihara *et al*., 1992, p. 50; Okumura and Karasawa, 1994, p. 72, pl. 19, figs. 1–9. [non *Mytilus coruscus* Gould, 1861]

Materials: Two immature and four mature well-preserved specimens (MFM16015–16020) from the Kubohara facies of the Toyama Formation, Iwamura Group at loc. Shimogahora.

Description: The shell is rather small for the species (ca. 140 mm in maximum length). The shell outline shows a considerable variation from an elongate form (Fig. 1G) to a broad form (Fig. 1F). In immature specimens, the fine radial striae on the exterior surface are not recognized (Fig. 1E) or faintly recognized only in the middle part of the ventral surface (Fig. 1C), and no crenulations are found on the interior margin (Fig. 1D). The fine radial striae are distinct all over the surface in some mature specimens, but in others

are not so distinct. The crenulations on the interior margin are visible in only a few specimens (Fig. 1I). Three marginal teeth on the subumbonal shelf are recognized in an immature specimen (Fig. 1D), but become obsolete with growth. The anterior adductor muscle scar is large, elongate and recognizable by its dark coloration. The posterior adductor and retractor muscle scars are continuous, but mostly damaged during the preparation.

Remarks: We compared the specimens from the Iwamura Group described here with well-preserved specimens of *Crenomytilus grayanus* from the lower Pleistocene Setana Formation in the Kuromatsunai area of Hokkaido. The shell characters of the Iwamura specimens agree well with those of the Setana specimens, although the former is smaller than the latter in shell size (the largest Setana specimens attain 180 mm in length; Y. Kamemizu, pers. comm., 2017).

Judging from published illustrations, the same collecting locality, and/or the same collecting unit (Kubohara facies), it is reasonable to assume that the specimens we examined and those examined by Shibata (1978), Ujihara *et al*. (1992) and Okumura and Karasawa (1994) from the Iwamura Group under the name of *M. coruscus* are conspecific and referable to *C. grayanus*. In addition, a mytilid specimen illustrated by Itoigawa *et al*. (1974, 1981, 1982) from the Akeyo Formation of the Mizunami Group under the name of *M. coruscus* is safely referable to *C. grayanus* in having the delicate radial ornaments (YK, pers. obs.; see Ando and Itoigawa, 2018).

Comparison: *Crenomytilus grayanus* is very similar to *Mytilus coruscus* Gould, 1861, the largest species of the genus in the northwestern Pacific, in shell size and form. However, *C. grayanus* is clearly distinguished from *M. coruscus* by having delicate radial striae on the shell exterior, fine crenulations on the interior shell margin, a gently convex dorsal margin, a widely developed inner nacreous layer on the shell interior, a non-vacuolated pseudonymph, and a larger and more elongate anterior adductor muscle scar (Figs. 2E–G, 3B). On the other hand, *M. coruscus* is characterized by its smooth shell exterior without radial ornament, its slightly concave dorsal margin, its smooth interior shell margin, its vacuolated pseudonymph, its thick inner nacreous layer with sparse pores on the shell interior, and its small semi-circular anterior adductor muscle scar (Figs. 2A–D, 3A). These characters strongly suggest that this species is safely assigned to the genus *Mytilus*.

Stratigraphic and geographic range: Fossil occurrences of *C. grayanus* are summarized in Table 1. Prior to this study, the oldest record of this species was from the lower middle Miocene Oya Formation of Tochigi Prefecture (Kurihara, 2010). The occurrence of this species from the Iwamura Group extends its oldest record back to the upper lower Miocene. This species also occurs from the contemporaneous Akeyo Formation of the Mizunami Group, Gifu Prefecture, and Hiramatsu Formation of the Awa Group, Mie Prefecture (Fig. 4).

This species is currently distributed on rocky bottoms from subtidal to a depth of 60 m, in northeastern Honshu and northwards, the Okhotsk Sea and Kurile islands, and in northeastern Korea and Russia (southern Primoriye region) (Higo *et al*., 1999).

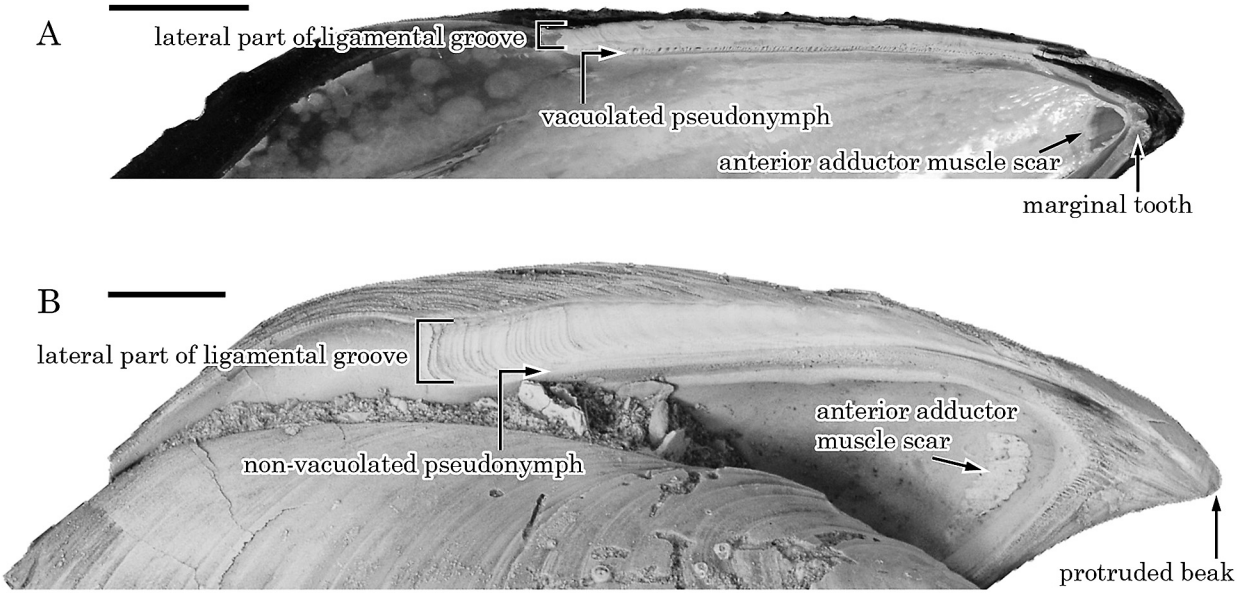


Fig. 3. Comparisons between the hinge plate and anterior adductor muscle scar of *Mytilus coruscus* Gould and *Crenomytilus grayanus* (Dunker). All scale bars 10.0 mm. **A, *M. coruscus*.** Interior view of left valve, MFM150001 from loc. Morai, Recent. **B, *C. grayanus*.** Interior view of left valve, MFM112461 from loc. Soibetsu, lower Pleistocene Setana Formation.

Table 1. Fossil occurrence of *Crenomytilus grayanus* (Dunker) in Japan.

Epochs and formations	Sources
Early Miocene	
Akeyo Fm., Gifu Pref.	This study; Ando and Itoigawa, 2018
Toyama Fm., Gifu Pref.	This study
Hiramatsu Fm., Mie Pref.	This study
Middle Miocene	
Oya Fm., Tochigi Pref.	Kurihara, 2010
Haraichi Fm., Gunma Pref.	Kurihara, 2010
Late Miocene	
Kubota Fm., Fukushima Pref.	Nomura and Hatai, 1936; Iwasaki, 1970
Itahana Fm., Gunma Pref.	Kurihara, 2010
Pliocene	
Sasaoka Fm., Akita Pref.	Ogasawara *et al*., 1986
Shigarami Fm., Nagano Pref.	Yokoyama, 1925b
Zukawa Fm., Toyama Pref.	Matsuura, 1985
Kume Fm., Ibaraki Pref.	Noda *et al*., 1993
Taga Group, Ibaraki Pref.	Yokoyama, 1925a
Pliocene or early Pleistocene	
Yunokogawa Fm., Aomori Pref.	Matsubara, 2009
Early Pleistocene	
Yuchi Fm., Hokkaido	Noda *et al*., 1984
Zaimokuzawa Fm., Hokkaido	Akamatsu and Suzuki, 1990
Setana Fm., Hokkaido	Sawada, 1962
Omma Fm., Ishikawa Pref.	Ogasawara, 1977; Matsuura, 1985

Discussion and conclusions

Careful observations of well-preserved specimens reveal that a large "*Mytilus*" that was previously assigned to *Mytilus coruscus* from the Toyama Formation of the Iwamura Group is actually referable to *Crenomytilus grayanus*. We confirmed the occurrence of *C. grayanus* from the contemporaneous upper lower Miocene formations in the Mizunami and Awa Groups. Itoigawa *et al*. (1981) listed "*M. coruscus*" from several other "eastern Setouchi Miocene Series" in central Japan. In our opinion, some of these specimens may be reidentified with *C. grayanus*, but others may be assigned to other species, including *Perna oyamai* Taguchi, 1983, a warm-water fossil mussel originally described from the lowermost middle Miocene Katsuta Group in western Japan.

Although fossil "*Mytilus coruscus*" has been reported from Miocene and Pliocene formations in northern and central Japan (see Noda, 1992, p. 60–61), most of the records are based on poorly preserved specimens. In our opinion, the unequivocal fossil record of *M. coruscus* is very sparse and limited to the Pleistocene (*e.g*., Kawase *et al*., 2015), and the Neogene fossil record of *M. coruscus* requires a taxonomic re-evaluation.

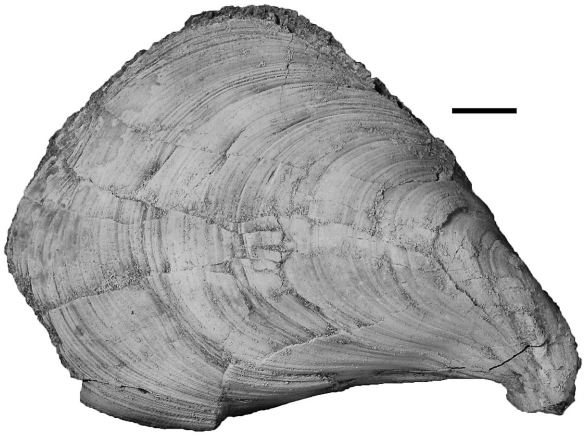


Fig. 4. ***Crenomytilus grayanus* (Dunker).** Exterior view of right valve, L: 92.9 mm, H: 67.5 mm, W: 23.5 mm, MFM41008 from loc. Mashino-Oike, upper lower Miocene Hiramatsu Formation, Awa Group, coated with ammonium chloride, scale bar 10.0 mm.

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Appendix

Localities cited

Mashino-Oike: Outcrop near the Mashino-Oike pond at Mashino, Iga City, Mie Prefecture, central Japan. 34°45.736'N, 136°16.9078'E. Hiramatsu Formation of the Awa Group. Age: upper lower Miocene. Leg. T. Kaede, early 2000s. [= Loc. 3 of Ozawa and Inoue, 2002].

Morai: Morai coast, Atsuta, Ishikari City, Hokkaido. 43°18.3491'N, 139°44.7266'E. Recent (beach washed). Leg. Y. Kurihara, 2004.

Shimogahora: Outcrop in the playground at Shimogahora, Yamaoka-cho, Ena City, Gifu Prefecture, central Japan. 35°21.8906'N, 137°23.519'E. Kubohara facies of the Toyama Formation, the Iwamura Group. Age: upper lower Miocene. Leg. Y. Kurihara, early 2000s. [= locality of Okumura and Karasawa, 1994].

Soibetsu: Right bank of Soibetsu-gawa River at Soibetsu, Kuromatsunai-cho, Suttsu County, Hokkaido. 42°41.163'N, 140°16.701'E. Setana Formation. Age: lower Pleistocene. Leg. R. Nakashima, date unknown; Y. Kurihara, 2015.