The Genus *Fulgoraria* (Gastropoda: Volutidae) of the northeastern Kamchatka Peninsula and Sakhalin Island, with Notes on the Paleoecology and Distribution of the Subfamily Fulgorariinae in the Oligocene of the northern Pacific

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ABSTRACT

Four new species of the genus *Fulgoraria* Schumacher, 1817, (subgenus *Musashia* Hayashi, 1960) are described from the Oligocene Alugian Formation of the Ilpinsky Peninsula, northeastern Kamchatka Peninsula, Russia. Previously described fulgorariine gastropods from the same region, and from the Oligocene of Sakhalin and Karaginsky Islands, are also figured. Oxygen isotopic analyses of contemporaneous *Cyclocardia* shells, along with a comparison of the ecology of Recent congeneric taxa and a paleoecologic analysis suggest a bathyal environment as most probable for these Oligocene Fulgorariinae. A review of the Oligocene biogeography of northern fulgorariines along the northern Pacific margin, including the western coast of North America, indicates that this subfamily had a much broader distribution during late Paleogene time than today. These data point to more favorable climatic conditions (including lower water temperatures) for dispersal of fulgorariine volutes during the Oligocene.

Key words: Fulgorariinae; systematics; distribution; Oligocene; Paleogene; Northern Pacific.

INTRODUCTION

Volutid gastropods are common as fossils in Cenozoic faunas of the northern Pacific region. However, their fossil record from some parts of this region, particularly the far east of Russia, is still very incompletely known. The subfamily Fulgorariinae Pilsbry and Olsson, 1954, is the dominant group among North Pacific Cenozoic volutes. Recent members of the "northern group" (Shikama, 1967) of this subfamily are restricted to Japan and adjacent seas. Less well-known extinct species occurred along both eastern and western margins of the North Pacific during both early and late Cenozoic time.

The subfamily Fulgorariinae comprises a group of carnivorous gastropods with a uniserial radula composed of tricuspid rachidian teeth (Cooke, 1922; Habe, 1943; Okutani, 1963; Weaver & du Pont, 1970; Watanabe & Habe, 1978). The higher systematics of this subfamily is still not fully resolved, with the two most recent revisions (Shikama, 1967; Weaver & du Pont, 1970) differing primarily in the ranking of supraspecific taxa. Shikama (1967) recognizes three genera: *Fulgoraria* Schumacher, 1817, *Musashia* Hayashi, 1960, and *Saotomea* Habe, 1943, as well as the subgenera *Psephaea* Crosse, 1871, *Nipponomelon* Shikama, 1967, *Neopsephaea* Takeda, 1953, and *Miopleiona* Dall, 1907. The last two are known only as fossils. Shikama's classification is based exclusively on shell characters such as the number and shape of columellar plaits, the size and form of the protoconch, and features of the external shell morphology. All of these characters, especially the number of columellar plaits, may vary during ontogeny. Interpreting this highly variable shell morphology is further complicated when working with fossil specimens, as they are often incompletely preserved.

Based on shell and radular characters, Weaver and du Pont (1970) recognized only a single Recent north Pacific genus *Fulgoraria*, with the subgenera *Psephaea*, *Volutipisma* Rehder, 1969, *Musashia*, *Kurodina* Rehder, 1969 and *Saotomea*. These authors regard *Nipponomelon* as a synonym of *Musashia*, and do not discuss the taxonomic position of the fossil *Neopsephaea* and *Miopleiona*.

The present paper provisionally follows the classification of Weaver and du Pont (1970), but includes *Nipponomelon*, *Miopleiona*, and *Neopsephaea* as subgenera of *Fulgoraria*.

Twenty-six species of Fulgorariinae from the latest Eocene and Oligocene formations of the north Pacific have been figured or described. Of these, eight are known only from North America [Poul Creek and Narrow Cape (of Sitkinak Island) Formations of Alaska; Blakeley, Twin River, and Eugene Formations of Oregon and Washing-

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ton], and have been referred to the subgenera *Nipponomelon*, *Musashia*, *Miopleiona*, and *Neopsephaea* (Durham, 1944; Addicott *et al.*, 1971; Tegland, 1933; Allison & Marincovich, 1981; Moore, 1984). Nine species, referred to the subgenera *Fulgoraria*, *Psephaea*, *Musashia*, *Nipponomelon*, and *Neopsephaea*, are restricted to the Oligocene of Japan (Ashiya, Kishima, Nishisonogi, Kumano, and Chikokubo Formations of Kyushu and Honshu Islands; Momijiyama Formation of Hokkaido) (Oyama *et al.*, 1964; Shikama, 1967; Masuda & Noda, 1976). An additional seven species, from various localities along the northwestern coast of the United States and the Kamchatka Peninsula, have only been identified to the subgeneric level (Allison & Marincovich, 1981; Moore, 1984; Gladenkov, Sinelnikova & Bratseva, 1987). Only one species endemic to the Kamchatka Peninsula and the Koryak Upland, *Fulgoraria* (*Musashia*) *olutorskiensis* L. Krishtofovich, 1973, has been described to date. A second Siberian species, *Fulgoraria* (*Nipponomelon*) *tokunagai* (Kanehara, 1937) is more widespread and is also known from the Oligocene of Japan.

MATERIALS AND METHODS

All specimens in this study were collected during field work in eastern Kamchatka and Sakhalin Island between 1965 and 1986. They were taken from the Alugian Formation of northeastern Kamchatka, the "*Laternula*" sandstones of Karaginsky Island, and the Matchigarian Formation of central Sakhalin (fig. 21). The preservation of the specimens was often fragmentary, with the figured specimens representing the most complete material.

In order to address the questions of the ecology of these Oligocene fulgorariines, a paleotemperature analysis of shells of *Cyclocardia ilpinensis* Pronina, 1973, which occurs in abundance in the same strata as the volutes, was conducted. This standard analysis was based on the ratio of the oxygen isotopes ($^{18}O/^{16}O$). The values of $^{18}O/^{16}O$ (PDB standard, mass spectrograph) were adjusted to the Standard Mean Ocean Water (SMOW) standard and corrected for altered isotopic composition at higher latitudes. Temperature values were calculated using the following formula:

$$T = 16.5 - 4.3\,(b - A) + 0.14(b - A)^2,$$

where T is the temperature in °C, b is the instrumentally determined difference in the $^{18}O/^{16}O$ ratio between the sample and the standard, and A is the correction for the original isotopic composition of sea water. For high latitudes $A = -1$. Prior to analysis, all shells were examined using X-ray diffraction analysis to exclude specimens in which the aragonitic structure had recrystallized.

The following institutional acronyms are used: GI—Geological Institute, Russian Academy of Sciences, Moscow; CMG—Central Museum of Geology, St. Petersburg, Russia; USNM National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

SYSTEMATICS

Family Volutidae Rafinesque, 1815
Subfamily Fulgorariinae Pilsbry and Olsson, 1954
Genus *Fulgoraria* Schumacher, 1817
Subgenus *Musashia* Hayashi, 1960

Fulgoraria (*Musashia*) *novoilpinica* **new species**
Figures 1, 2, 17

Description: Shell fusiform, slender, with 4–5 postnuclear whorls. Last whorl stout, comprising ⅔ of shell height. Suture moderately impressed, subsutural band absent. Aperture elliptical (Length/width ≃ 3). Inner lip with one narrow columellar fold and siphonal fold. Siphonal canal wide. Axial sculpture of numerous (10–12 on penultimate whorl) thin ribs, more pronounced on earlier whorls, smoother and wider on body whorl. Spiral sculpture of fine, raised threads covering entire surface.

Material examined: Holotype—USNM 468649, length (incomplete) 119.5 mm, width 58.3 mm; Paratype—GI 4072, length (shell strongly decorticated) 124.7 mm, width 62.2 mm; 1 juvenile shell, 7 broken shells and fragments, 2 molds; all from the type locality.

Type locality: Northwestern part of the Ilpinsky Peninsula, eastern Kamchatka, Russia. Upper part of the Alugian Formation, Oligocene.

Stratigraphic range: Known only from the Upper part of the Alugian Formation of eastern Kamchatka. Oligocene.

Comparative remarks: Although similar to *Fulgoraria shutoi* Shikama, 1967, from the Kishima Formation (Oligocene, Japan), this new species differs in having a more elongated last whorl, narrower axial folds, nearly smooth body whorl, and only a single fold rather than several strong ones.

Fulgoraria (*Musashia*) *olutorskiensis* (L. Krishtofovich, 1973)
Figures 11, 12, 15, 16

Miopleiona oregonensis Khomenko, 1933:25, pl. 6, fig.20.
Miopleiona olutorskiensis L. Krishtofovich, 1973:77, pl. 22, figs. 8,9.
Musashia olutorskiensis Devyatilova & Volobueva, 1981:128, pl. 32, fig. 2.

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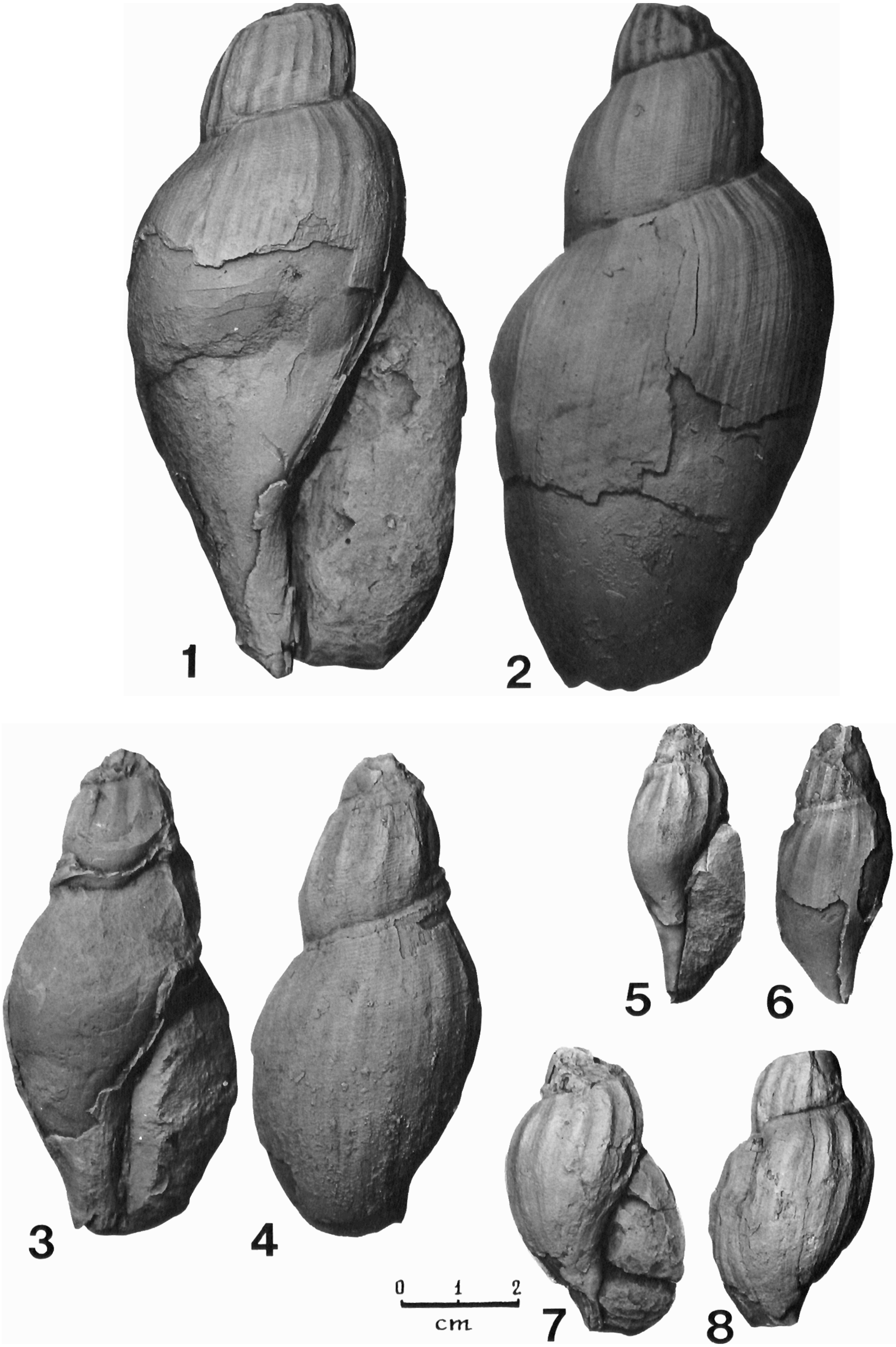
Figures 1, 2. *Fulgoraria* (*Musashia*) *novoilpinica*, new species. Holotype, USNM 468649, 119.5 mm, Alugian Formation, Oligocene. **Figures 3, 4.** *Fulgoraria* (*Musashia*) *genuata*, new species. Holotype, USNM 468650, 84.5 mm, Alugian Formation, Oligocene. **Figures 5, 6.** *Fulgoraria* (*Neopsephaea*) *tenuis* (Shikama, 1967). GI 1164, 49.2 mm, Matschigarian Formation, Oligocene. **Figures 7, 8.** *Fulgoraria* (*Musashia*) *tilitschikensis*, new species. Holotype, USNM 468652, 51.1 mm, Alugian Formation, Oligocene.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Musashia (Musashia) sp. Gladenkov, Sinelnikova & Bratseva, 1987:57, pl. 15, fig.2.

Description: Shell oblong, fusiform, relatively thin, with 5–6 postnuclear whorls. Body whorl comprises approximately ⅔ of shell height. Suture slightly depressed, with narrow subsutural band. Aperture elliptical, acute posteriorly. Inner lip arched, with one narrow columellar fold. Callus thin, narrow. Shell surface nearly smooth, with thin growth striae and very fine, raised spiral threads.

Material examined: Holotype—CMG 21/10285, length 130.4 mm, width 48 mm, Pachatchi River, Olutorsky Region, eastern Kamchatka, Russia, "Ilpinian" Formation, Oligocene; Paratype—19/10285, Gulf of Olutorsk, Govena Peninsula, eastern Kamchatka, Russia, Oligocene; GI 1486, GI 4055—both from Ilpinsky Peninsula, northeastern Kamchatka, Russia, Alugian Formation, Oligocene; 9 incomplete shells and fragments and 7 molds.

Type locality: Olutorsky Region, northeastern Kamchatka, Russia.

Stratigraphic range: Known from the Oligocene formations of northeastern Kamchatka; abundant in the Alugian Formation of the Ilpinsky Peninsula.

Comparative remarks: With its nearly smooth sculpture, this species most closely resembles *Fulgoraria* (*Musashia*) *nagaoi* (Shikama, 1967) from the Poronai Formation (Eocene–Oligocene of Hokkaido), but differs in being more elongated, in having fine spiral sculpture, and in having a distinct subsutural band.

Fulgoraria (*Musashia*) *genuata* **new species**
Figures 3, 4, 19

Description: Shell oblong, fusiform, slender, with three stout, preserved whorls, and estimated 5–6 postnuclear whorls in intact specimens. Body whorl comprises < ⅔ total shell length. Suture shallow, slightly impressed. Aperture elliptical. Columella with one weak columellar fold. Sculpture of straight, smooth, widely spaced axial ribs (4 per whorl), most prominent on early whorls. Spiral sculpture of numerous, fine, slightly raised threads covering shell surface.

Material examined: Holotype—USNM 468650, length 84.5 mm, width 40.0 mm; Paratype—GI 40721, length 75.9 mm, width 46.1 mm; both from type locality.

Type locality: Northwestern part of Ilpinsky Peninsula, northeastern Kamchatka, Russia. Alugian Formation. Oligocene.

Stratigraphic range: Known only from the Alugian Formation of the Ilpinsky Peninsula. Oligocene.

Comparative remarks: Although similar to *Fulgoraria* (*Musashia*) *fujimotoi* (Kanno, 1958) from the Hikokubo Formation (Oligocene-Miocene, Japan), this new species differs in having stouter whorls and a lower spire, in having one instead of two columellar folds, and in having finer spiral sculpture.

Fulgoraria (*Musashia*) *cordata* **new species**
Figures 13, 14

Description: Shell elongate, fusiform, slender, with four postnuclear whorls, short siphonal canal and narrowly channeled suture. Body whorl comprises approximately ¾ of shell length. Aperture oblong, with narrow posterior angle. Columella with one weak columellar fold. Axial sculpture of low, rounded ribs ($\simeq$ 12 per whorl on penultimate whorl). Axial ribs crossed by fine, closely spaced spiral lines.

Material examined: Holotype—USNM 468651, length 59.1 mm, width 24.3 mm; Paratype 1—GI 4063/2, length 50.5 mm, width 26.5 mm; Paratype 2—GI 40531, length 62.8 mm, width 26.5 mm; two molds, three fragments and one impression; all from the type locality.

Type locality: Northwestern part of Ilpinsky Peninsula, northeastern Kamchatka, Russia. Upper part of the Alugian Formation. Oligocene.

Stratigraphic range: Known only from the type locality.

Comparative remarks: This new species is most similar to *Fulgoraria* (*Musashia*) *weaveri* (Tegland, 1933) of the Blakeley Formation (Oligocene, Washington, USA), but has a more elongated shell, more numerous axial ribs, and much stronger spiral threads.

Fulgoraria (*Musashia*) *tilitschikensis* **new species**
Figures 7, 8, 18

Description: Shell globosely fusiform, solid. Teleoconch of about 5 whorls. Suture narrowly pressed. Body whorl comprises ⅔ shell length. Aperture semiovate, with thin, narrow callus. Inner lip with one weak, subvertical columellar fold. Axial sculpture of rounded arcuate ribs (13 on body whorl). Spiral sculpture lacking.

Material examined: Holotype—USNM 468652, length (incomplete) 51.1 mm, width 29.5 mm, from the type locality; Paratype GI 40724, length (incomplete) 65.0 mm, width 37.6 mm, Ilpinsky Peninsula, northeastern Kamchatka, Russia. Alugian Formation, Oligocene.

Type locality: Korf Settlement, Coal River, northeastern Kamchatka, Russia. Alugian Formation. Oligocene.

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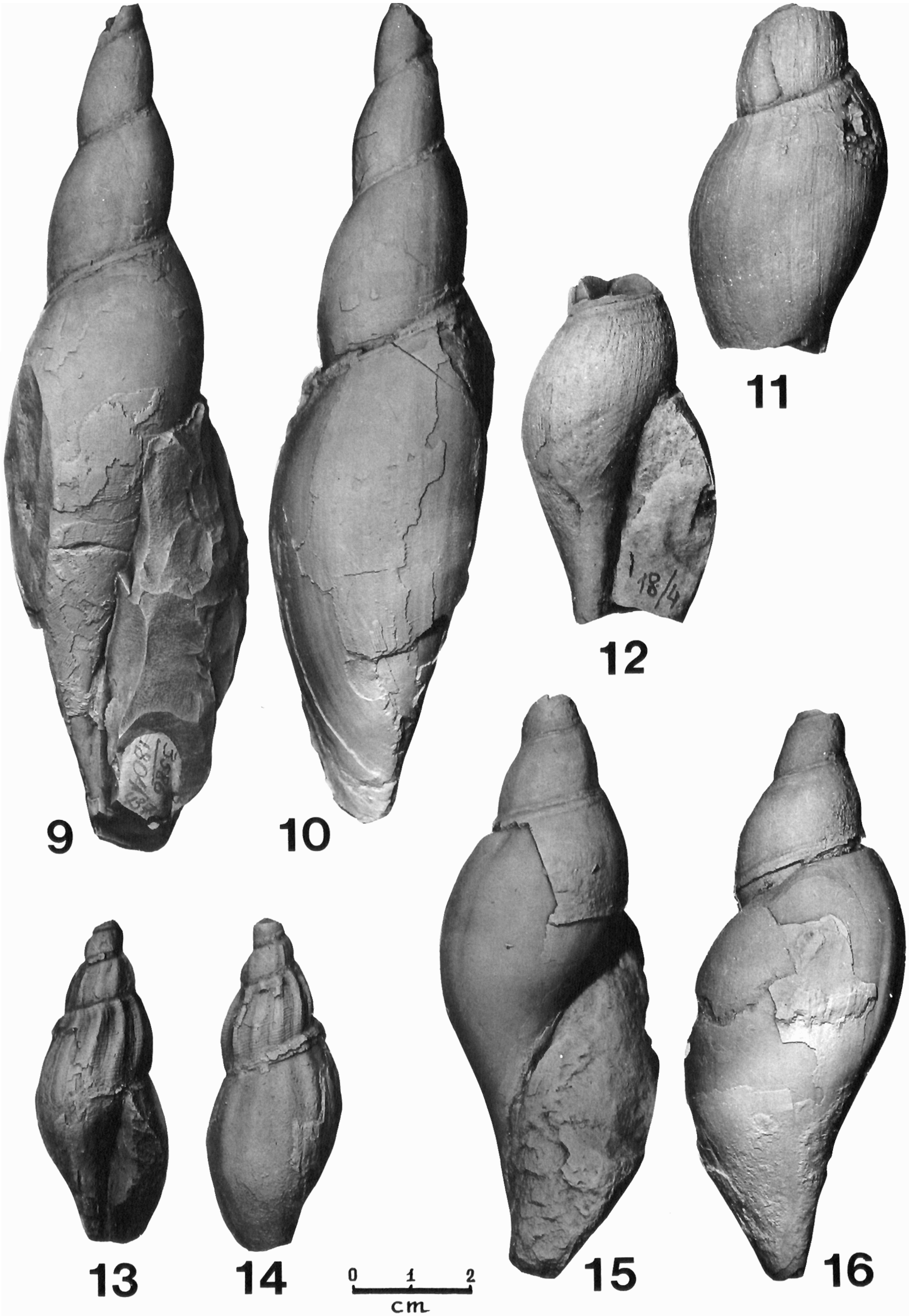
Figures 9, 10. *Fulgoraria* (*Nipponomelon*) cf.*tokunagai* (Kanehara, 1937). GI 3586/1804, 149 mm, "*Laternula*" Sandstones, Karaginsky Island, Oligocene–Lower Miocene (?). **Figures 11, 12, 15, 16.** *Fulgoraria* (*Musashia*) *olutorskiensis* (L. Krishtofovich, 1973). **11, 12.** GI 1486, 61.8 mm, **15, 16.** GI 4055, 103.9 mm, Alugian Formation, Oligocene. **Figures 13, 14.** *Fulgoraria* (*Musashia*) *cordata*, new species. Holotype, USNM 468651, 59.1 mm, Alugian Formation, Oligocene.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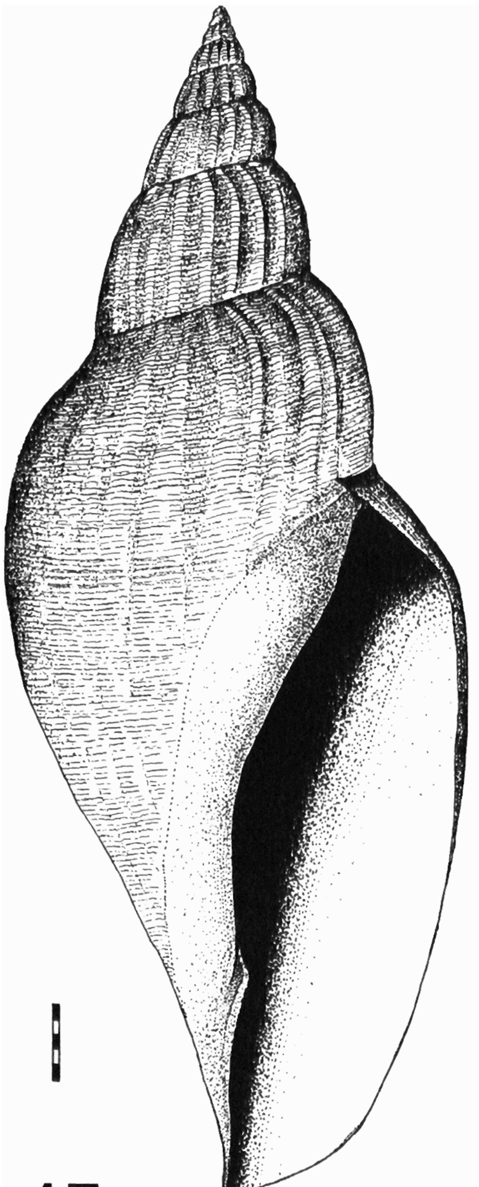

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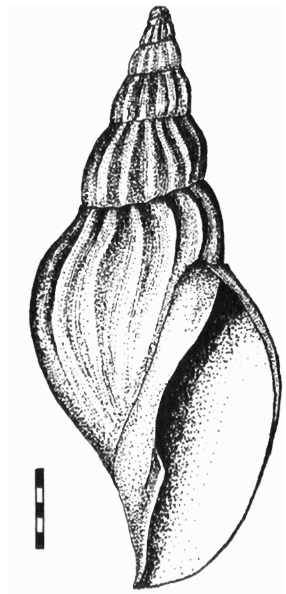

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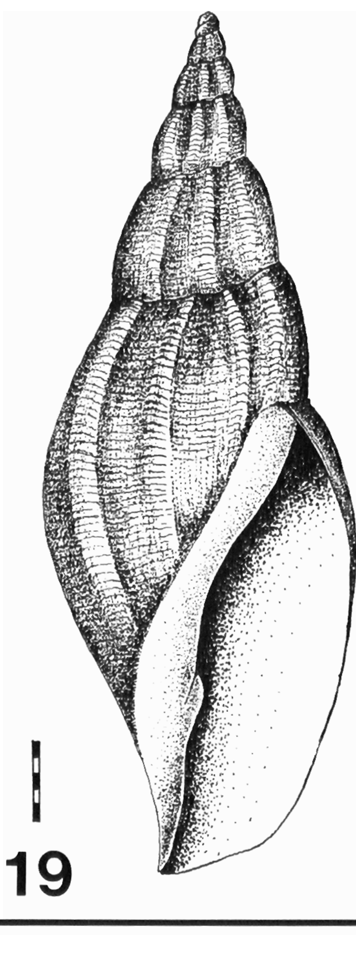

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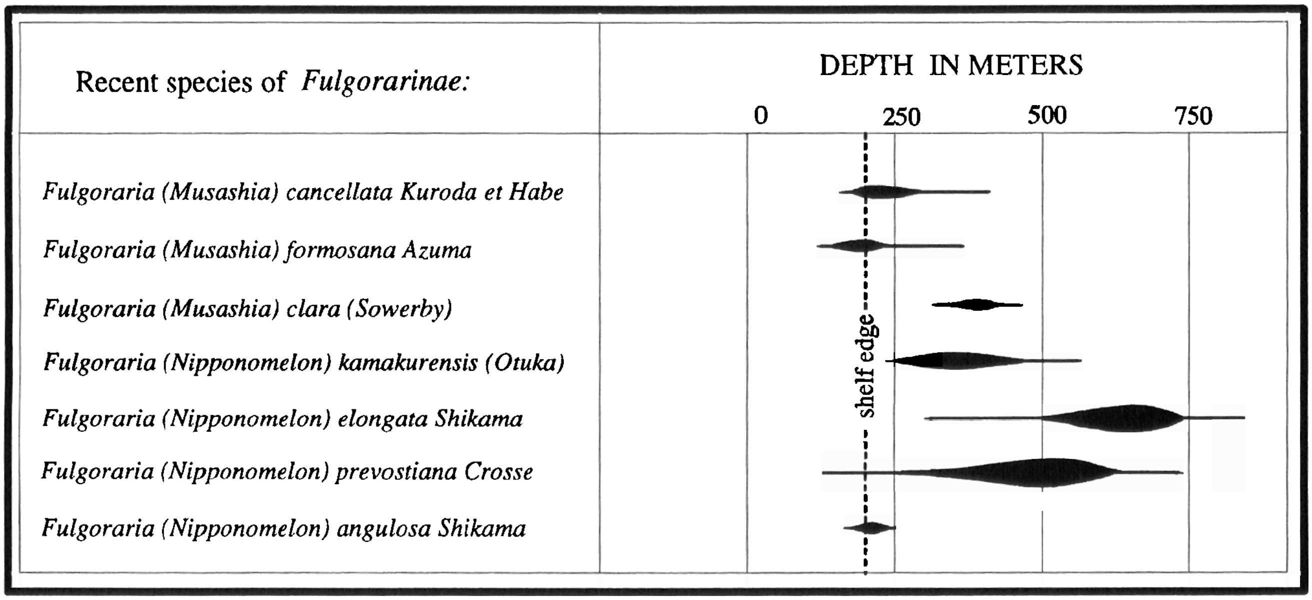

Figure 20. Bathymetric distributions of Recent species of Fulgorariinae of Japan and adjacent seas, based on data in Shikama (1967), and Weaver and du Pont (1970). Thickness of lines indicates relative abundance.

Stratigraphic range: Known only from the Alugian Formation of northeastern Kamchatka, Russia. Oligocene.

Comparative remarks: This species resembles *Fulgoraria* (*Musashia*) *shikamai* Moore, 1984, from the Poul Creek Formation (Alaska, USA) and the Clallam and Twin River Formations (Washington, USA), but this new species has more sharpened axial ribs and finer spiral threads.

Subgenus *Nipponomelon* Shikama, 1967

Fulgoraria (*Nipponomelon*) cf. *tokunagai* (Kanehara, 1937)
Figures 9, 10

Psephaea tokunagai Kanehara, 1937:16–18, pl.2, figs. 2–5.
Fulgoraria (*Psephaea*) *prevostiana* Crosse, Shikama, 1954:pl.6, fig. 26.
Fulgoraria tokunagai Kamada, 1962:192, pl.21, figs. 5–8.
Musashia (*Nipponomelon*) *tokunagai* Shikama, 1967:100–101, pl.14, fig. 4.
Musashia tokunagai Devyatilova & Volobueva, 1981:128, pl.33, fig. 1.

Original Description: "Shell tall and high spired, apical angle about 25 degrees. Suture slightly impressed with narrow shelf around it. Surface ornamented with axial folds, which may be somewhat accentuated above and tend to disappear on the body whorl. Spirally grooved regularly, also over the folds. Aperture spindle shaped, obliquely notched posteriorly, with narrower anterior canal. Inner lip provided with two columellar folds and covered by a thin callus, which adheres to the columella and thickens anteriorly."

Material examined: One specimen, GI 3586/1804, length 149 mm, width 62.2 mm, from the "*Laternula*" sandstones, Karaginsky Island, Gnunvayam River, Russia. Oligocene-Lower Miocene (?).

Type locality: Yanagaya bed, Nagakura coal mine, Yumoto, Iwaki City, Fukushima Prefecture, Honshu, Japan. Lower Miocene.

Stratigraphic range: "*Laternula*" sandstones, Karaginsky Island, Gnunvayam River, Russia, Oligocene-Lower Miocene (?), to Yanagaya bed, Nagakura coal mine, Yumoto, Iwaki City, Fukushima Prefecture, Honshu, Japan. Lower Miocene.

Comparative remarks: *Fulgoraria tokunagai* is characterized by a large size, high spire, large protoconch, and numerous axial folds. The spiral sculpture on the single specimen from Karaginsky Island is poorly preserved, but this specimen retains visible traces of the axial folds and thin spiral grooves. The shape and size of this specimen, especiallv the features of the aperture, suture, and sculpture, are the same as in typical *F. tokunagai*. However, the Russian specimen differs from the type in having a single columellar fold rather than two. This difference, together with the poor preservation of this shell puts the species determination of this specimen in some doubt.

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Figure 17. *Fulgoraria* (*Musashia*) *novoilpinica*, new species. Reconstructed drawing of holotype. **Figure 18.** *Fulgoraria* (*Musashia*) *tilitschikensis*, new species. Reconstructed drawing of holotype. **Figure 19.** *Fulgoraria* (*Musashia*) *genuata*, new species. Reconstructed drawing of holotype. Scale bars = 10 mm.

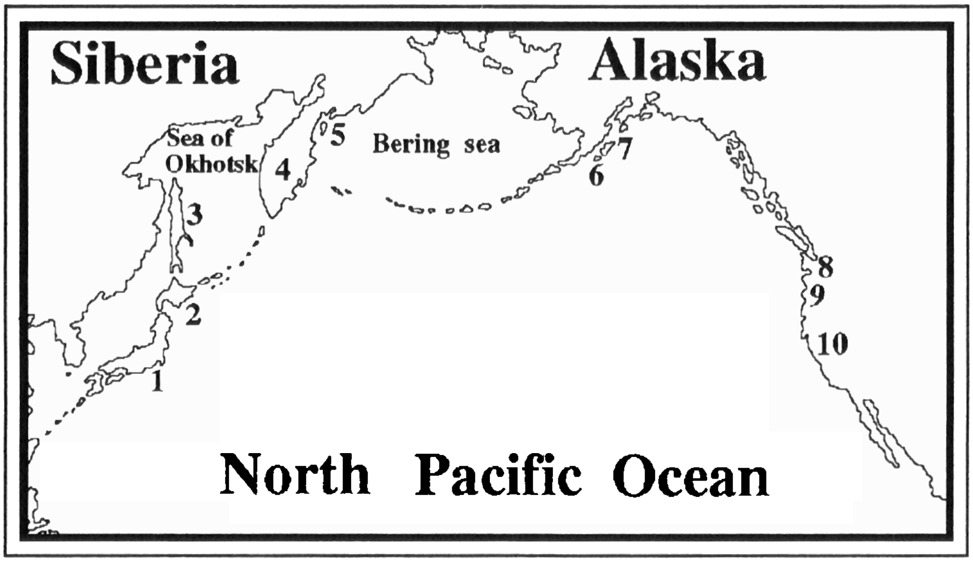

Figure 21. Fossil localities of Oligocene Fulgorarinae in the North Pacific referred to in the text. 1—Honshu Island, 2—Hokkaido Island, 3—Sakhalin Island, 4—Kamchatka Peninsula, 5—Karaginsky Island, 6—Sitkinak Island, 7—Kodiak Island, 8—Oregon, 9—Washington, 10—California.

Subgenus *Neopsephaea* Takeda, 1953

Fulgoraria (*Neopsephaea*) *tenuis* Shikama, 1967
Figures 5,6

Musashia (*Neopsephaea*) *tenuis* Shikama, 1967:116–117, pl.13, figs. 3,4.

Original description: "Shell small in size, slender, fusiform and with low spire. Suture shallow and there is no subsutural band. Last whorl vaulted at middle and aperture relatively narrow. Surface of whorl smooth and axial ribs relatively few and weak, about 11 in penultimate whorl, gradually becoming obsolete anteriorly. Tip of columella straight and narrow. There may be one columellar plait".

Supplemental description: Shell is rather slender, elongate, fusiform, with about 5 (when restored) whorls separated by a shallowly impressed suture. Body whorl and aperture comprising slightly more than ⅔ of total shell length. Aperture elliptical, forming acute angles at anterior and posterior margins. Siphonal notch relatively narrow. Outer lip thin, simple. Columella with one weak columellar fold. Callus very thin. Shell surface smooth,

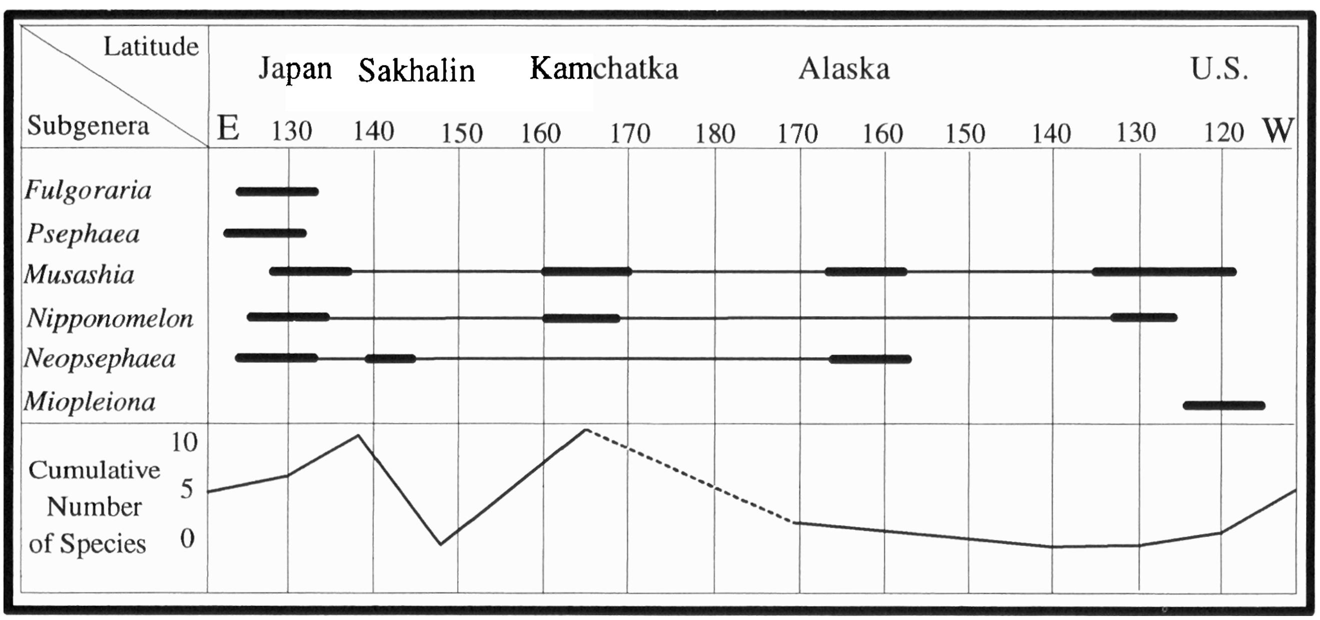

Figure 22. Geographic distribution of the subgenera of *Fulgoraria*, and their species diversity during the Oligocene.

with thin growth lines. Axial sculpture of low, rounded ribs (11–12 on body whorl) that disappear on anterior portion of body whorl.

Material examined: One specimen, GI 1164, length 49.2 mm, width 22 mm, near Lake Matschigar, central Sakhalin Island, Russia. Matschigarian Formation. Oligocene.

Type locality: Zochuku Sandstone, Kishima Group, Nagasaki Prefecture, Kyushu, Japan. Oligocene.

Stratigraphic range: Near Lake Matschigar, central Sakhalin Island, Russia, Matschigarian Formation, Oligocene, to Zochuku Sandstone, Kishima Group, Nagasaki Prefecture, Kyushu, Japan, Oligocene.

Comparative remarks: This species is closely allied to *Fulgoraria* (*Neopsephaea*) *antiquior* Takeda, but may be distinguished by its more swollen body whorl, narrower aperture with distinctive posterior margin, smooth surface, and axial ribs that are fewer in number or entirely obsolete.

DISCUSSION

The lithology of the Alugian Formation of the Ilpinsky Peninsula in eastern Kamchatka consists of gray to dark gray claystones and clays. This formation has a total thickness of about 950 meters, and is continuous, lacking hiatuses or internal unconformities. No shallowing or deepening trends are evident within the section. The strata contain numerous carbonate concretions ranging in size from 1 cm to several meters. Some of the claystone beds are delicately laminated. These types of sediments are indicative of soft bottom environments.

Molluscan remains are quite common, but are not concentrated in particular layers or lenses. Fossils occur sporadically throughout the section, both in concretions and within the matrix. The molluscan fauna does not exhibit many changes from the bottom to the top of the formation. These data point to a depositional regime comprising relatively rapid and uninterrupted sedimentation (Kidwell, 1988).

Species diversity in the molluscan assemblage of the Alugian Formation is low. The most abundant taxa occurring together with fulgorariine volutes include *Trominina bicordata* (Hatai & Koike, 1957), *Trominina ishikariensis* (Hayasaka & Matsui, 1951), *Neptunea ezoana* Takeda, 1953, *Bathybembix sakhalinensis korjakensis* Volobueva, 1981, *Optoturris* (?) *sp.*, *Turritella sp.*, *Cryptonatica spp.*, *Acila praedivaricata* Nagao & Huzioka, 1941, and *Cyclocardia ilpinensis* Pronina, 1973. All these taxa have relatively broad bathymetric ranges, occurring from lower neritic to bathyal depths (Hall, 1960; Noda, 1975; Scarlato, 1981; Moore, 1984).

Recent species of Fulgorariinae are mainly bathyal animals, dredged most often from depths of 250 to 700 or more meters (fig. 20). Bathymetrically, the bathyal zone extends from a mean depth of 200 m to 2000 m, and thermally, from the 15°C isotherm in low latitudes down to the −3°C isotherm in high latitudes. Substrates are predominantly fine silts, muds, and oozes (Encyclopedia of Oceanography, 1974; Hickman, 1974). Oxygen isotope analyses of five *Cyclocardia ilpinensis* shells collected from the bottom through the top of the Alugian Formation allowed the estimation of paleotemperatures as ranging from 3°C to 5°C. These data indicate that water temperatures remained quite uniform during the deposition of this formation, and support the hypothesis of a bathyal environment. When compared to Recent bathyal bottom temperatures, these data suggest that the climatic conditions during Alugian deposition were similar to those found between 32°N and 45°N, and approximate the temperatures that define the distribution of Recent species of *Fulgoraria*. Paleotemperatures estimated for the Alugian Formation exhibit some correlations with those estimated for Oligocene formations of the western coast of North America. Paleotemperatures of the Blakeley Formation (*Echinophoria apta* zone), which contains five species of Fulgorariinae, were estimated as to be 5–8°C. The remains of *Aturia* nautiloids in great abundance, which may have required a temperature of at least 16°C could be explained by postmortem transport of empty shells, which is fairly common with Recent *Nautilus*. Paleodepth was thought to range from 100 m to 350 m (Moore, 1984). Similarly, the Narrow Cape Formation of Sitkinak Island (Alaska), which contains three species of Fulgorariinae , was deposited in the outer neritic zone of the continental shelf (Allison, 1978). A comparison of the Narrow Cape data with that of Recent Alaskan mollusks suggests a paleodepth of 100–200 m, and water temperatures of 10–12°C in summer months during the Oligocene (Allison & Marincovich, 1981). According to Hall (1964), this type of marine climate can be defined as cool-temperate. The Recent species *Fulgoraria* (*Nipponomelon*) *prevostiana* (Crosse, 1878) has been dredged from depths of 110–732 m off western Hokkaido, Japan, at a bottom temperature of 11.8°C (Weaver & du Pont, 1970:45). Water temperatures for the Alugian Formation thus seem to be colder than those in western America. These data more probably suggest a deeper depositional environment for the Alugian Formation, perhaps no shallower that 400–500 m, and therefore colder water.

Oligocene climatic conditions, therefore, must have been quite favorable for a wider distribution of fulgorariine volutes that is seen today. This is clearly supported by the fossil record (fig. 21). Based on the stratigraphic distribution and analysis of total species diversity of Cenozoic volutes, it has been deduced that the Oligocene–Early Miocene was the first period of wide distribution and high species diversity of northern Pacific Fulgorariinae (Oleinik, 1990). There was, however, an appreciable amount of endemism, especially at the subgeneric level. *Fulgoraria s.s.* and *Psephaea*, for example, were restricted to the western Pacific, while *Miopleiona* is known only from the northeastern Pacific. These restricted geographic ranges may have been caused by different centers of origin of the North Pacific Fulgorariinae, or were the results of differing dispersal strategies. Other subgenera, such as *Musashia* and *Nipponomelon*, were abundant throughout the north Pacific. Total species diversity of Fulgorariinae, however, did not vary appreciably during the Oligocene of the north Pacific (fig. 22).

ACKNOWLEDGMENTS

I thank Dr. Yuri B. Gladenkov and Dr. Valentina N. Sinelnikova, of the laboratory of Phanaerozoic Stratigraphy of the Geological Institute of the Russian Academy of Sciences, for providing material; Dr. Sergei I. Kiyashko, of the Institute of Marine Biology in Vladivostok for the oxygen isotope analyses. Photographs of the shells were taken by Mr. Andrew A. Okunev of the Geological Institute, Moscow. My special thanks to Dr. M. G. Harasewych, National Museum of Natural History, Smithsonian Institution, Washington, D.C., Dr. E. J. Petuch, Florida Atlantic University, Boca Raton, Florida, and Dr. L. K. Marincovich, U.S.G.S., Menlo Park, California for critical review of the manuscript.

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